

*OLD FIELD FOREST SUCCESSION
IN THE SWEDISH WEST COAST
ARCHIPELAGO*



Gunilla Olsson

*Department of Plant Ecology
University of Lund, Sweden*

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Träden följer inte musiken Vi
 följer trädens musik,
dansande, över bergen, hög-
 landets krön
Träden är nu vår klingande tröskel
 Krönet mot avgrunden
Där, långt borta, finns havet, silver-
 glänsande

G. Sonnevi 1983

Sedan jag varit på åtskilliga holmar och ingenting
märkvärdigt funnit, kom jag om aftonen till Lindö. ...

P. Kalm 1742

The dissertation is based on the following four papers:

- I. Olsson, E. G. 1984. Old-field succession - an introduction.
- II. Olsson, E. G. 1984. Effects of field layer vegetation on old field forest succession in the Swedish west coast archipelago.
- III. Olsson, E. G. 1984. Obstacles to birch colonization in old fields.
- IV. Olsson, E. G. 1984. Effects of regenerative strategy on old-field forest succession.

Reference to these papers is made by using the respective Roman numerals.

On the small coastal island of Lindö in the Swedish west-coast archipelago, 26 arable fields abandoned 23 - 41 years preceding the time of the study showed 0 - 100% tree colonization. The investigations were focused on the factors influencing the initial pattern of tree colonization on the abandoned fields.

A brief review of previous old field studies and main factors shown to be influential for the secondary succession, as well as a general description and some historical comments on the study area, are given (I). The following factors are discussed in relation to the colonization of trees in the old fields:

1. Field layer plant communities (II)

Classification (TABORD) and reciprocal averaging ordination of field layer vegetation not colonized by shrubs and trees resulted in six vegetation types, ranging from species-rich calcareous meadow vegetation, through communities dominated by introduced species (i.e., originating from seed mixtures for leys, weeds, etc.), to wet meadows dominated by a few tall perennials. The mean and total number of species per plot decreased with increasing time from abandonment, but the content of introduced species was not age-related. Nor was the latter variable related to colonization by trees.

The vegetation types dominated by tall perennials showed no tree colonization at all, indicating that these types may be resistant to tree colonization, at least within the investigated time interval. However, several plots belonging to other vegetation types resisted tree colonization within the same time interval. It is assumed that the field-layer vegetation acts as a structural barrier against establishment of tree seedlings.

No correlation between time since abandonment and tree colonization was found. Fields of the same age with respect to abandonment displayed all degrees of forest development, ranging from 0 - 100% canopy cover.

2. Soil conditions (II)

The variation in species composition between different types of field layer vegetation is largely ascribed to the

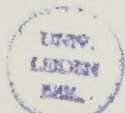
great variation in soil conditions, ranging from dry and sandy humus-poor soils to clayey and wet organic soils. These differences are also demonstrated by the range in loss on ignition for the soil samples, and thus implicitly in water-holding capacity.

Using rough soil characteristics, based on the classes sandy soil, clayey soil and wet organic soil, and testing against tree colonization did not show any correlation.

3. Former land use (III, IV)

Former land use - either former arable field used for ley cropping or former pasture - was shown to be influential for tree colonization due to the different types of field-layer structure produced. The leys were provided with a well-developed sward and subsequently with a considerable litter layer. However, the pastures, were left with the sward partly wounded by trampling and selective cattle grazing, thus having a number of "safe sites" for the colonizing seeds. This is demonstrated on Lindö by the pastures colonized by Betula verrucosa Ehrh. and Betula pubescens Ehrh. and Pinus silvestris L. close to the time of abandonment, while no abandoned field was colonized by these species (IV).

The hypothesis of the sward as a structural barrier against tree colonization was experimentally tested in two old fields (III). Although there was access to adjacent birch seed sources, the old fields lacked birch colonization even 31 and 39 years after abandonment. Plots cleared from



field-layer vegetation were exposed to the spontaneous birch seed rain. Seed rain, seed germinability and soil conditions were also examined. In one of the fields, Betula seedlings colonized the plots and survived for more than one year. In the other field, with soil of lower water holding capacity, no seedlings appeared and neither did sowing result in any colonization. It is concluded that two different factors acted as obstacles to birch colonization: 1/ the grass sward as a structural and competitive barrier, and 2/ soils with low humus content and thus low water-holding capacity (III).

4. Area of the abandoned field (IV)

Field or pasture area had no influence on the number of colonizations by tree species. Nor did field or pasture area show any relationship with the density of colonizations, except for animal-dispersed tree species, in which case there was a weak negative relationship, viz., the smaller the fields, the more successful the colonizations.

5. Availability of diaspore sources, distance from dispersal sources and regenerative strategy (IV)

The positions of individuals, assumed to be potential sources of dispersal, were determined for each one of the tree species studied, as well as the distance from each dispersal source to the nearest field or pasture border. The species involved were also classified according to their regenerative strategy (i.e., type of regeneration).

The effects of A/ "number of nearby diaspore sources", B/ "regenerative strategy", C/ "distance to diaspore sources", and D/ "land use" on the success of colonization was tested for the 12 ligneous species. Of the total variation (ANOVA), 50% was accounted for by factors B-D. "Regenerative strategy" was the most important (accounting for 36% of the variation), followed by "distance to sources" (22%) and "land use" (4%). Exchanging the variable "distance to sources" for "number of nearby diaspore sources" accounted for 60% of the total variation; "number of sources" contributed 34%.

The dispersal modes ranked as follows in terms of colonization success within the old fields: vegetative regeneration > wind-dispersed group with small seeds > animal-dispersed > wind-dispersed with medium-sized seeds.

Old fields left as leys at abandonment are provided with a sward which acts as a structural barrier against colonization by trees with small wind-dispersed seeds. Without disturbances which produce breaks in the sward, such old fields on this island can remain uncolonized for 40 years. When the sward degenerates, for example, by overshadowing by adjacent tree canopies, tree colonization can occur by wind-dispersed species with medium-sized seeds, such as Tilia cordata Mill. and Fraxinus exelsior L. Vegetatively regenerating species, such as Populus tremula L., with great suckering ability, and animal-dispersed species, such as Quercus robur L., "planted" in the sward and having large endosperms, both have good possibilities for successful establishment in old fields as well

as in abandoned pastures. At distances exceeding 10 m from the dispersal source, there is a pronounced decrease in colonizing success for all dispersal groups. The most distance-dependent is, of course, the vegetatively regenerating group, while the animal-dispersed group is the least susceptible.

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Kumar revised the language.

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I OLD-FIELD SUCCESSION - AN INTRODUCTION

1. OLD-FIELD SUCCESSION - HISTORICAL BACKGROUND

Old fields have been a favourite object of study by workers on secondary plant succession during the 1900s. Most of the studies, especially the early ones, were performed in North America. These were mainly descriptive accounts of the early successional stages (Crafton & Wells 1934; Quarterman 1957 etc). In the literature on succession of old field vegetation, several authors have stressed the importance of species composition, structural complexity and diversity of vegetation, soil conditions, etc. within each seral stage as essential for the development of the succeeding stage. These papers all follow a Clementsian tradition (Clements 1916), with considerable elements of determinism (cf. Oosting 1942; Bonck & Penfound 1945; Quarterman 1957; Odum 1960; 1969). Opposed to this tradition is the "individualistic concept" (sensu Gleason 1926) which holds that successional result from different life-history characteristics and population dynamics within each population of participating species (cf. Egler 1954; Drury & Nisbet 1973; Pickett 1976; 1982; Peet & Christensen 1980).

The most common method of analysis has been to make simultaneous studies of fields abandoned at different times and thus of different successional stages (Bard 1952; Bazzaz 1968; Hanks 1972). Long term studies of permanent plots have been made only in a few cases (Schmidt 1981; Pickett 1982; Collins & Adams 1983).

One of the first to introduce an experimental approach in the old field studies was Catherine Keever (1950), with her classical study of the annual changes in plant dominants during the first five years of old-field succession in North Carolina. Her results, which pointed towards the great importance of life cycles of the populations of species involved in the succession, have been influential for the development of the "individualistic concept".

The questions of species turnover and diversity of species during old-field succession (Hurd et al 1971; Nicholson & Monck 1974; Bazzaz 1975; Tramer 1975; Hard 1976; Squires & Wistendahl 1977; Pickett 1982) as well as studies of primary production in old-field succession (Odum 1960; Wiegert & Evans 1964; Golley & Gentry 1966; Wiegert & McGinni 1975; Jukola-Sulonen 1983) have been thoroughly studied. Diversity on old fields used for ley cropping is initially low, increases rapidly during the first 10 years (Jukola-Sulonen 1983) and reaches a maximum during the early forest stage (Bazzaz 1975). The total number of species attains a maximum at stages with simultaneous presence of weeds, "introduced species" and resident species and decreases at stages with shrub and tree invasion (Hard 1976). It seems difficult to reveal general trends for the old-field primary production. The contradictory results may partly be due to use of different crops preceding abandonment (Jukola-Sulonen 1983).

During the 1970s, an increasing amount of experimental studies were directed towards ecophysiological questions (Bazzaz 1974; Parrish & Bazzaz 1976; 1982; Peterson & Bazzaz 1978; Zangerl & Bazzaz 1983) and population dynamics (Kroh & Stephenson 1980; Gross & Werner 1982; Goldberg & Werner 1983; Tremmel & Peterson 1983). Greater flexibility in ecophysiological attributes indicating broader niches in earlier stages of succession was found (Bazzaz & Carlson 1982).

Recently, studies have been increasingly directed towards effects of seed dispersal by animals on old field succession. Although the pioneer field-work on this subject (Janzen 1970; 1971) was performed in tropical forests, the results showed the great importance of the relationships between seed dispersal and animals, relevant also for old-field successions in temperate regions. In this context, seed dispersal by birds (Debussche; Escarré & Lépart 1982), fruit types and maturity time (Stiles 1980; Herrera & Jordano 1981), and structural complexity of the old fields (McDonnell & Stiles 1983), are some of the subjects that have been studied.

Secondary succession on old fields has frequently been used to formulate models for succession theories (Egler 1954; Odum 1960; 1969; Drury & Nisbet 1973; Pickett 1976; van Hulst 1978; 1979; Peet & Christansen 1980). Although Clements (1916) had a profound influence upon the theories of secondary succession, Clementsian theories were mainly based upon observations of primary succession. Experimental verification of the theories is still sparse (Hils & Vankat 1982).

Scandinavian old-field studies are relatively scanty. The work of Kalela (1961) and Jensen (1978), performed in archipelagos in southern Finland and Denmark, respectively, are relevant to the subject of this thesis. Kalela demonstrated the importance of field size and presence of open ditches for the course of tree colonization. Jensen's study (1978) showed the great resistance to tree invasion by grass- and Epilobium-dominated areas.

Succession processes and theories have frequently been reviewed (Drury & Nisbet 1973; Horn 1974; Golley 1977; Connell & Slayter 1977; Bazzaz 1979; Gorham, Vitousek & Reiners 1979; Liljelund 1979; McIntosh 1980; West & Shugart 1981; Keever 1983).

2. FACTORS INFLUENCING THE COURSE OF SECONDARY SUCCESSION

In the extensive literature on secondary succession touched upon in the previous paragraphs, the factors found to determine the course of secondary succession vary considerably from study to study. A variety of factors have thus been shown to influence the course of succession in abandoned fields. The following paragraphs briefly present the most important ones:

1. Field-layer plant communities

The field-layer species can ameliorate (Egler 1954: "relay floristics" , Connell & Slayter 1977: "facilitation model") or impede (Connell & Slayter 1977: "the inhibition model") the establishment of later species such as trees and

shrubs. The processes involved are suggested, for example to be simple space relationships (pre-emption of available space), influencing the possibilities for germination of seeds and development of seedlings. Other processes can be related to chemical components derived from plants that inhibit or stimulate the growth of invading species (allelopathic compounds). Such substances may also inhibit the growth of nitrogen fixing and nitrifying bacteria (Rice & Panchohy 1972; Rice 1976; Smith & Rice 1983) and thus influence the successional sequence.

2. Soil conditions

Such conditions may be soil moisture (cf. Raynal & Bazzaz 1973; Pickett & Bazzaz 1978; Bornkamm & Hennig 1982) or residual effects of manure (Thomsen Jr 1943; Hanks 1971).

3. Former land use

The former crop, e.g. grain or hay, combined with or free from subsequent grazing, can be important in relation to establishment of new species (cf. Beckwith 1954; Bazzaz 1968; Hanks 1971; Schmidt 1981).

4. Availability of diaspore sources

This factor can be important, especially on island localities. Frequencies of the colonizers should reflect the composition of the surrounding species (for tree species, cf McQuilkin 1940; Schmidt 1981).

5. Distance to diaspore source

The establishment of new species can be positively correlated to decreasing distance to the diaspore source (cf. Spring, Brewer et al. 1974; Debussche, Escarré & Lepart 1982).

6. Area of the abandoned field

A small-sized field will be colonized (by trees) within a shorter time than a large-sized one (cf. Kalela 1961; Spring, Brewer et al. 1974).

7. Regenerative strategies of the invading species

The mode of dispersion and the mode of regeneration, e.g., vegetative propagation and/or sexual regeneration, can influence the time relationship and the species structure of the colonizing species (Grime 1981; Debussche, Escarré & Lepart 1982; Howe & Smallwood 1982; McDonnell & Stiles 1983).

In this thesis, the succession processes related to the establishment of shrub and tree species will be emphasized. Parts of paragraphs 1 and 2 above will be discussed in paper 2; paragraphs 3 - 5 will be dealt with in paper 3; and paragraphs 4 - 7 will be discussed in paper 4.

3. THE STUDY AREA - GENERAL DESCRIPTION

The field observations for the present study was performed on the island of Lindö in the province of Bohuslän on the Swedish west coast (Fig. 1). The island has been protected as a nature reserve since 1970 due to its species-rich vegetation, containing several rare species, and also to its beautiful small-scale, coastal landscape, strongly influenced by traditional farming activities.

The archipelago zone along the coast here is narrow. Lindö, together with the interconnected islands of Kalvö and Trossö, are the outermost islands used as farming areas. Only some islets and skerries exist west of these islands. The shortest distance from Lindö to the mainland is 1.5 km but the nearest island is only 600 m distant. The islands of Lindö, Kalvö and Trossö today make up an interconnected island chain formed by the ongoing land upheaval, estimated here to be 40 cm per century (Atlas över Sverige 1953). The length of the island chain is about 6.5 km and the maximum breadth of Lindö is 2 km. The islands jointly cover a total area of 531 ha, of which Lindö accounts for 178 ha.

A characteristic feature of the islands is extensive areas of rocky plateaus, with missing or shallow layers of mineral soil, intermingled with fissure valleys of different shapes, giving the islands a broken topography. The bedrock consist of red granite, rich in potassium feldspar, which is weathered to a very small extent (Asklund 1947). The troughs of the valleys are covered by deep marine deposits consisting mainly of sand

and, to a lesser extent, of marine clays. Marine shells are frequently intermingled in these layers and appear as extensive deposits of pure shells, especially in the border zones near the valley slopes (Hessland 1943). The eastern parts of the islands have a relatively sheltered position and the valley mouths here are bordered by salt marshes, in contrast to the western shores dominated by exposed rocks. Maximum elevation (37 m a s l) is attained at the eastern part of Lindö. All parts of these islands are situated below the borderline for the postglacial regression.

The temperature climate is maritime with low amplitudes within the year. The mean annual temperature is about $+7.7^{\circ}\text{C}$ (long-term mean 1931-1960 for the island of Ursholmen, 10 km north-west of Lindö; official records of the Swedish Meteorological and Hydrological Institute). February is the coldest month (mean -1.4°C) and July is the warmest (mean $+17.5^{\circ}\text{C}$). The mean annual precipitation is 608 mm (long-term mean 1931 - 1960 for Ursholmen). The distribution of precipitation over the year is shown in Table 1. Snow falls almost regularly during winter but the number of days with snow cover varies considerably between years; completely snow free winters also occur.

In this part of Scandinavia a mixed deciduous woodland would be the potential forest vegetation (Fries 1951). Oak forest (Quercus robur L.) with elements of hazel (Corylus avellana L.), birch (Betula verrucosa Ehrh. et B. pubescens Ehrh.), aspen (Populus tremula L.) and, to a lesser extent, ash (Fraxinus excelsior L.) and lime (Tilia cordata Mill.)

would be the most frequent woody species. Some elements of pine (Pinus silvestris L.) might also be present since Lindö is situated near the border between two climatic forest types - the nemoral, broad-leaved deciduous and the boreo-nemoral forest zones (Sjörs 1971; Walter 1979).

The coastal part of Bohuslän was covered with mixed deciduous forest with oak as dominating species as late as around 1650 (Atlestam 1942). Apart from fish, timber was a principal export commodity, and about 100 sawmills existed in the province (Atlestam 1942). Increasing exploitation of the forest took place from that time onwards. Recurrent periods of fishing for herring during the 1600s, 1700s and the 1800s led to heavy withdrawal of timber and fuel required for the numerous salt industries and tryworks in the coastal areas. In the 1700s, most of the forests in coastal Bohuslän had been exploited, resulting in extensive areas of Calluna heathlands on the rocky plateaus (Holmberg 1867; Lindner 1935; Fries 1958). These areas were intensively used as grazing areas for cattle and sheep. To improve the production of Calluna for grazing purpose, the heathlands were regularly burned (Holmberg 1867; Lindner 1935; Atlestam 1942; Fries 1958). In general, winters are relatively warm, allowing a prolonged cattle grazing period over the year (Kalm 1742; Sjöbeck 1933; Atlestam 1942). The practice of using small-sized short-term tillages in the the heathlands was induced by a severe shortage of manure in the permanent arable fields (Kalm 1742; Fries 1958; Bringeus 1963). Moreover, there was a pronounced shortage of fuel during the 18th and 19th centuries. Juniper (Juniperus communis L.) and heather along with

turf and wreckage was collected and used as fuel (Kalm 1742; Lindner 1935; Atlestam 1942; Fries 1958; L. Martinsson pers. comm.). All these factors worsened the prospects for forest revival in the coastal areas.

The islands of Lindö and Kalvö reflections this general trend. During the 19th and early 20th centuries, Lindö and Kalvö were severely exploited for cultivation and fishery purposes. Fishing, together with small-scale supporting farming, provided the main livelihood on Kalvö, while the reverse relationship was valid on Lindö. In the late 1800s, Lindö harboured 10 families living on a combination of farming and fishing, while Kalvö had 30 families living mainly by fishing (Dalén 1941). At this time there were 20 and 30 heads of cattle, respectively, at Lindö and Kalvö, and a total of 100 sheep and 10 horses (Ivarsson 1971). All sediment areas that could be cultivated were ploughed and used for growing crops. Grass for hay was harvested by mowing the salt marshes (Gillner 1960; L. Martinsson pers. com.), several small hilly grasslands, zones bordering the fields, and some wooded meadows. The intensive land use on Lindö during the 1860s is shown in Fig. 2. During the period 1860 - 1935 there was a continuous increase in the area of arable fields at the expense of the area of the mown meadows; the ratio arable fields/ meadows changed in Lindö during the same time from 1.9 to 5.4. The area of the meadows decreased from 6.4 ha in 1861 to 2.9 ha in 1936 (Land Survey maps; Länsstyrelsen, Göteborg).

This intensive utilization of nature resulted in complete deforestation. During the late 1800s only one diminutive grove

of oak, lime and hazel, sheltered by the highest hill, and one wooded meadow remained on Lindö (Lantmäteriakt 521; Länsstyrelsen, Göteborg; Karlström 1982). Kalvö was totally deforested. However, at border zones along the infields, certain tree species, such as lime (Tilia cordata Mill.), oak (Quercus robur L.), ash (Fraxinus excelsior L.), hazel (Corylus avellana L.) and occasionally aspen (Populus tremula L.), were preserved. These species were regularly coppiced or pollarded, producing fuel and nutrient-rich fodder for sheep and cattle, as well as raw materials for bast and agricultural tools (Kalm 1742; Sjöbeck 1959; Holmberg 1867; Rackham 1980).

From 1930 onwards there was a progressive decrease in farming activity in these coastal areas. Most of the farmers on Lindö and Kalvö ceased running the farms during the period 1945 - 1950. Only two farmsteads on Lindö were kept running until 1956 and 1957, respectively. The fields were then abandoned. The exceptions to this were two fields on the southern part of Lindö and some rocky areas and pastures on Kalvö which were used as grazing lands for sheep during the period 1961 - 1975 and after 1978 onwards. A distinguishing feature of the 26 investigated arable fields on Lindö and Kalvö is that they were used for ley cropping 2-4 years preceding abandonment, thus being provided with a well-developed sward at the time of abandonment (E. Andersson; L. Martinsson pers. comm.).

Previous botanical studies on Lindö were performed by Ivarsson (1971a). He described the deciduous shrubs and forest vegetation (mainly outside the old fields) and connected field layer vegetation from a phytosociological viewpoint. Secondary

succession in an abandoned wooded meadow was studied by (Ivarsson (1971b) and Karlström (1982). Hallberg (1971) investigated field layer vegetation and soil conditions on shell deposits in Lindö and other coastal parts of Bohuslän province.



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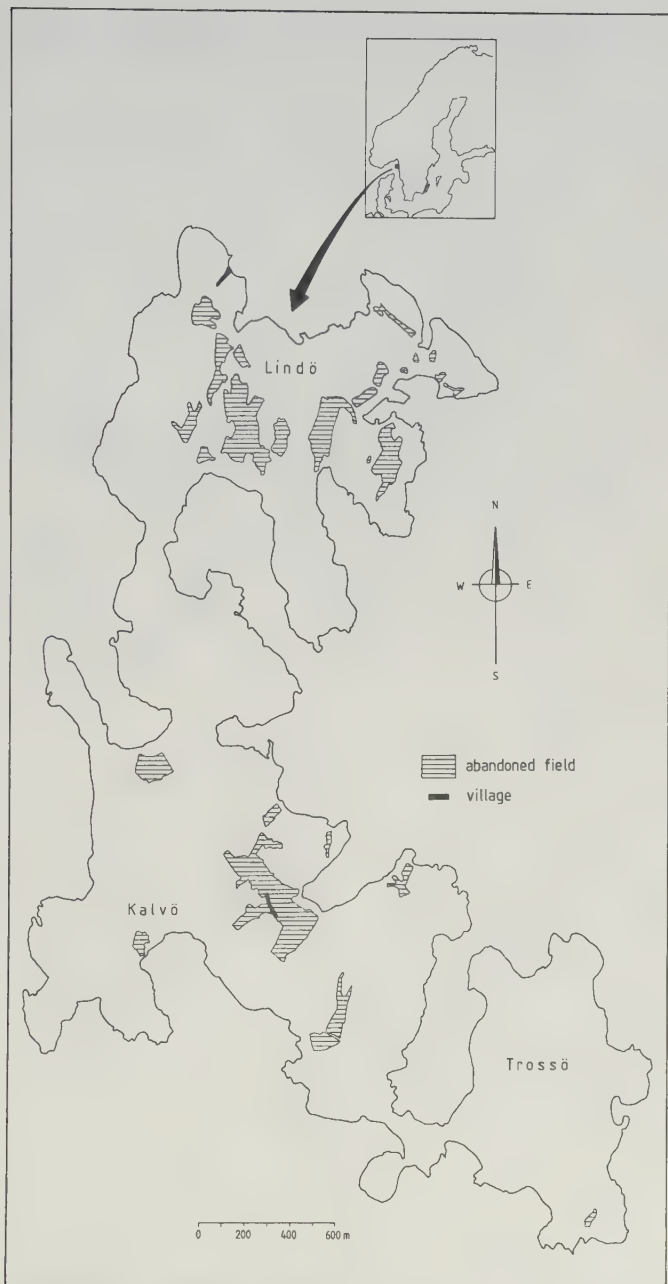


Fig. 1. The investigation area, the island of Lindö off the Swedish west coast.

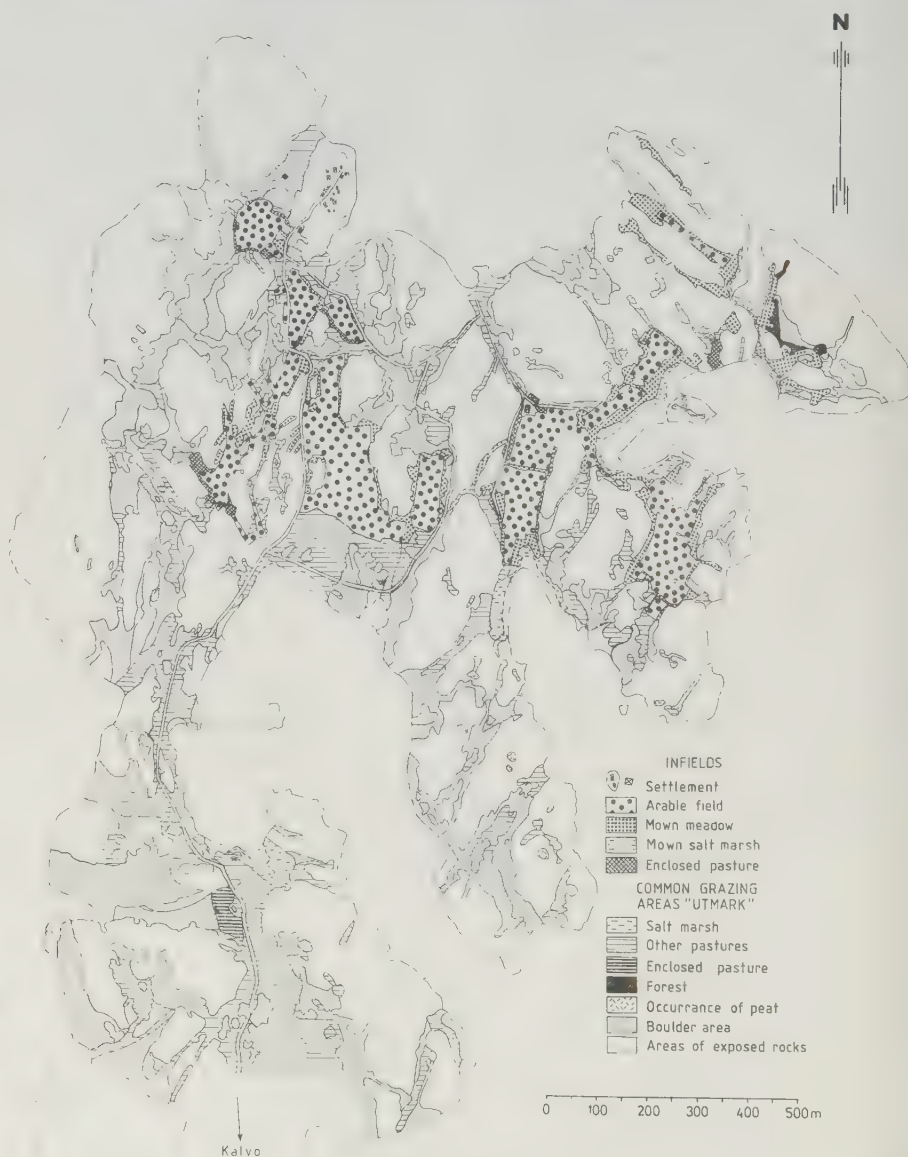


Fig. 2. Land use on Lindö 1861; compiled from Land Survey map 1861-1869 (Lantmäteriakt No. 521. 1861-1869; Lantmäterienheten, länsstyrelsen, Göteborg).

Table 1.
Distribution of rainfall during the year at the island Ursholmen, 10 km NW of Lindö (longterm mean 1931-1960, the Swedish Meteorological and Hydrological Institute; official records).

Season	Precipitaion mm	Percent of annual mean
Winter (Dec-Feb)	144	24
Spring (Mar-May)	97	16
Summer (Jun-Aug)	171	28
Autumn (Sep-Nov)	198	33

II. EFFECTS OF FIELD LAYER VEGETATION ON OLD-FIELD FOREST
SUCCESSION IN THE SWEDISH WEST-COAST ARCHIPELAGO

ABSTRACT

The influence of the composition of field layer species and soil conditions on tree colonization was investigated in 21 old fields abandoned 23 - 38 years preceding the study. The field layer vegetation was sampled by means of 67 plots containing 597 sample quadrats 1 m^2 or 4 m^2 in size, using species cover estimates. Classification (TABORD) and reciprocal averaging ordination of plots not colonized by shrubs and trees resulted in six vegetation types, ranging from species-rich calcareous meadow vegetation, through communities dominated by introduced species and weeds, to wet meadows dominated by a few tall-statured perennials. Another classification and ordination procedure included plots uncolonized, as well as plots partly or fully colonized, by shrub and tree species. Two new groups were formed, consisting mainly of plots with canopy cover $>50\%$, but these groups showed great mutual differences with respect to the field layer composition. Forty-eight percent of the colonized plots were classified into already existing groups, indicating that the tree colonization had not caused considerable change to the field layer composition. The types of vegetation that were dominated by tall perennials showed no tree colonization at all. This indicates that vegetation of these types might be resistant to tree colonization, at least within the time interval investigated. However, since several plots belonging to other types of vegetation resisted tree colonization within the same time interval, it is assumed that the field layer vegetation acts

like a structural barrier, irrespective of species composition.

No correlation between time since abandonment and tree colonization was found. Fields of the same age with respect to abandonment displayed all degrees of forest development, lying within the range 0 - 100% canopy cover. Nor were soil conditions found to be related to tree colonization.

The mean and total number of species per plot decreased with increasing time from abandonment, but the content of introduced and weed species was not age-related. Nor was the latter variable related to colonization by trees.

Since no clear connection was found between the pattern of tree colonization in the old fields and the field layer vegetation or soil conditions, it is concluded that the causes for this pattern must be sought in other factors related directly to the modes of regeneration of the actual tree populations.

1. INTRODUCTION

On the small island of Lindö (178 ha) in the Swedish west-coast archipelago, 21 arable fields were abandoned during the period 1942 - 1957. Of these fields, some are currently covered completely by young forests while others are not forested at all. To find an explanation for this apparent stochastic pattern, a plausible approach could be to focus on the field layer plant communities and the soil conditions in the old fields.

According to the viewpoint of Clements (1916), the species composition in one successional stage changes the environment and makes it more favourable for a specific succeeding stage. Plant communities in the field layer then ameliorate the possibilities for establishment of "later" species, e. g., tree species. This is expressed by Connell & Slayter (1977) as the "facilitation model" for successional changes. Opposed to this is the "inhibition model" (Connell & Slayter 1977), which suggests that certain plant communities impede establishment of new species. "The first occupants preempt the space and will continue to exclude or inhibit later colonists until the former die or are damaged." It is also frequently hypothesized that soil conditions influence the tree colonization. Such a soil characteristic could be soil moisture, influencing the extent and rate of invasion by new species (cf. Thomson, Jr. 1943; Raynal & Bazzaz 1973; Pickett & Bazzaz 1978; Bornkamm &

Hennig 1982).

A series of investigations were performed to study the factors behind the observed differences in tree colonization of old fields on Lindö (Olsson 1984a, 1984b). In this paper, the influence of the structure of field layer species and soil conditions upon the pattern of tree colonization of the abandoned fields is discussed.

2. THE STUDY AREA

The island of Lindö, the investigation area, is situated off the northern part of the Swedish west-coast ($58^{\circ}47'N$, $6^{\circ}54'E$). The archipelago zone here is very narrow. Lindö and the connected islands of Kalvö and Trossö, forming an island chain, are the outermost islands used for farming purposes. The distance to the mainland is 1.5 km, but the nearest island is only 600 m distant. The islands jointly have a total area of 531 ha, of which Lindö covers 178 ha (Fig. 1). The length of the island chain is 6.5 km and the maximum breadth of Lindö is 2 km.

Extensive areas of rocky granite plateaus, with missing or shallow layers of mineral soil alternating with fissure valleys of different sizes, impart a broken topography to the islands. The troughs of the valley are covered by deep marine deposits, consisting of sand and, to a lesser extent, of clay, intermingled with marine shells. The former arable fields are localized to these valleys.

The temperature climate is maritime, with low amplitudes during the year. February is the coldest month, with a mean of -1.4°C ; July is the warmest (mean $+17.5^{\circ}\text{C}$) and the yearly mean is 7.7°C (long-term mean 1931-1960 for the island of Ursholmen, 10 km north-west of Lindö. Swedish Meteorological and Hydrological Institute; official records). The mean annual precipitation is 608 mm at Ursholmen. The seasons of highest and lowest precipitation are September-November and March-May, respectively, accounting for 33% (198 mm) and 16% (97 mm) of the yearly amount. Snow falls fairly regularly during winter, but the number of days with snow cover varies considerably between years.

In this part of Scandinavia, mixed deciduous woodland is regarded as constituting potential forest vegetation (Fries 1951). Oak (Quercus robur L.) with elements of hazel (Corylus avellana L.) and, to a lesser extent, ash (Fraxinus excelsior L.) and lime (Tilia cordata Mill.) would be the most frequent woody species. Birch species (Betula verrucosa Ehrh. et B. pubescens Ehrh. and aspen (Populus tremula L.) occur as successional stages. Some elements of pine (Pinus silvestris L.) might also be present since Lindö is situated at the border between two climatic forest types: the nemoral, broad-leaved deciduous forest and the boreo-nemoral forest zone (Sjörs 1971; Walter 1979).

Of the 30 arable fields on Lindö and Kalvö, 21 were investigated for the purpose of this paper. These fields, ranging in size between 0.15 and 1.18 ha (mean 0.56 ha; SD 0.271), were

abandoned during the period 1942 - 1957. Although the fields were used for rotated cropping, including cereals, ley and potatoes, the last crop on all the fields during 2 - 5 years preceding abandonment was ley. Fertilizers were used in a very low amount during this terminal period. The leys consisted of perennial grasses, dominated by Phleum pratense L., Festuca pratensis Huds. and the leguminous forb Trifolium pratense L. Some patches of Arrhenatherum elatius (L.) J. et C. Presl. and Dactylis glomerata L. also occurred. In 1980, when this investigation was performed, the range of tree colonization in the old fields was 0 - 100% crown cover for the colonizing shrubs and tree species.

Border zones of 3-7 m width surround the fields. These zones were unploughed and unfertilized, but were regularly mowed. They served as a refuge for the resident flora of the traditional rural landscape in this region and, since abandonment, have acted as dispersal sources for colonization into the old fields.

The areas in between the old fields consist of formerly grazed rocky plateaus, now dominated by Calluna heathlands with scattered, expanding groves of pine and deciduous forest species previously mentioned.

3. METHODS

3.1. Sampling of vegetation

Vegetation analysis was performed on 21 abandoned fields and in the zones bordering 4 of these fields. Since the pattern of tree colonization pattern varied from uncolonized fields, through all intermediate stages, to a dense thicket of shrubs and young forest, the sampling areas were assigned to three categories. The term "forested plot" applies to areas colonized by shrubs and trees with crown cover $>50\%$; 4 m^2 sample quadrats were used here. For "shrubby plots" (scattered colonization of shrubs and trees and crown cover $<50\%$) and "uncolonized plots", the sample quadrat size was 1 m^2 . The term "uncolonized plot" is used below to refer to areas not colonized by shrubs and trees. The term "plot" designates the sampling area (of varying size and shape) within the fields in which the sample quadrats were distributed. The latter were distributed as follows within the plots: a/ 10 to 14 quadrats, randomly distributed within an area of $10 \times 10 \text{m}$; or b/ 5 - 14 quadrats, evenly spaced along transects of varying length. For the forested plots and the border zones, only the latter sampling design was used.

The whole data set from the abandoned fields consists of 67 plots, containing altogether 521 1 m^2 quadrats and 49 4 m^2 quadrats. The border zones were sampled by means of 4 plots consisting of 27 quadrats (1 m^2). The total number of quadrats is thus 597.

Cover estimates according to a modification of the Hult-Sernander-Du Rietz scale were used as quantitative estimates of species importance. The scale has the following degrees: 6 (100-75%), 5 (75-50%), 4 (50-25%), 3 (25-12.5%), 2 (12.5-6.3), 1 (less than 6.3%), + (solitary occurrence).

Information about former land use and time from abandonment was collected by interviewing landowners and former farmers and by studying local maps and documents.

3.2. Soil sampling

Depths of the soil layers and their physical properties were determined in each vegetation analysis plot. In soil data evaluation, a rough classification was made on the basis of three characteristics, viz., sandy soil, clayey soil and wet organic soil. A separate interpretation of tree colonization in relation to this soil classification was performed for each plot using the χ^2 -test (Wonnacut & Wonnacut 1972).

In 13 different vegetation analysis plots, representing six of the fields, five soil cores (203.6 cm^3) from the upper humus layer (0 - 5 cm) were collected. Measurements of pH, water content and loss on ignition, were performed in the laboratory. The concentrations of Na, K, Ca, Mg, N and C were determined. Water content and loss on ignition were determined gravimetrically by drying to 105°C and 400°C , respectively. For nitrogen determination, a semimicro Kjeldahl digestion was used. Soil carbon content was analysed by means of a "Leco carbon determinator CR 12" (Leco Corp., Michigan, U.S.A.). Determination of pH was performed in KCl solution, and Na, K,

Ca and Mg contents were determined by atomic absorption spectrophotometry.

3.3. Classification and ordination procedures

The vegetation data was classified by means of the TABORD program (Persson 1977; van der Maarel, Janssen & Louppen 1978), with similarity ratio (Wishart 1969) as similarity coefficient. This performs an agglomerative clustering of quadrats or plots and produces a structural phytosociological table of such clusters or groups. The initial classification was attained through the divisive, monothetic information drop method of Lance and Williams (1968), program DIVINF.

For technical reasons, the large total number of sample quadrats (597 quadrats) made a simultaneous classification based upon individual quadrats impossible. The material was therefore divided into three subsets, classified separately, viz., quadrats from the 1/ uncolonized, 2/ shrubby and 3/ forested plots. Cover estimates of species in the field layer from each quadrat were used in these classifications. Comparison between classifications of individual quadrats based upon cover estimates versus classification of plots, based upon arithmetic mean cover, revealed good agreement in quadrat/plot assignment and vegetation characteristics of clusters obtained. The vegetation data analyses discussed below are therefore based upon arithmetic mean cover for the plots and thus make a joint classification possible.

The data set from the 42 uncolonized plots, and the four plots from border zones (in all 383 sample quadrats) was classified

together (C1) using field layer mean cover per plot. A joint classification (C2) of all the uncolonized, shrubby and forested plots, but excluding the border zone plots, was also performed. It was based upon mean cover per plot. In these classifications, all shrubs and tree species were excluded, however, to avoid their influence upon the formation of the vegetation groups. Cluster formation in all classifications was exclusively founded on the composition of field layer species.

Ordinations were accomplished using the reciprocal averaging method (RA ordination) (Hill 1973; Gauch Jr., Whittaker and Wentworth 1977; Gauch Jr. 1982; Jukola-Sulonen 1983). Rescaling of the axes was performed using the square root of the quotient: estimated eigenvalues for each axis divided by the estimated eigenvalue for axis 1 (Clymo 1980). Ordinations were based upon the same data, viz. arithmetic mean cover for plots, as used in the C1 and C2 classifications, respectively. However, since eight plots originating from wet meadow vegetation strongly biased a good separation of the main group along the first axis in the RA ordination, these "wet" plots were excluded in the ordination of the joint set. The coordinates for the plots on the first two ordination axes were used to test for possible correlations between the vegetation and soil characteristics, time from abandonment and fraction of "introduced species", respectively.

The species in the vegetation groups, obtained from the classifications and ordinations, were separated into two subgroups: one containing "resident species" (R), i.e., species belonging to the resident flora of the old rural landscape in

this region; and another consisting of "introduced species" (I), i.e., species originating from seed mixtures for leys, weed species and other non-resident species favoured by intensive cultivation and manuring (Lyttkens 1885; Hård af Segerstad 1924; Hylander 1943; Fogelfors 1979; Souminen 1979; Malmgren 1982).

4. RESULTS

4.1. Vegetation classifications

Classification of the uncolonized plots (C1) resulted in six groups (groups 1 - 6, Table 1) containing in all 144 field layer species, while the joint classification (C2) (Table 2) resulted in eight groups (171 field layer species), six of which were the same as those obtained from the C1 classification. The two new groups (groups 7,8) consisted mainly of totally forested plots (>50% canopy cover). Remaining shrubby and forested plots were classified into already existing groups in the C1 classification, viz., groups 1 - 4. The addition of these plots did not alter the species composition from the C1 classification to any considerable extent, indicating that several forested plots had a composition of field layer species largely similar to that of uncolonized plots. The following description of species composition, etc., refers to groups obtained in the C1 classification, except for groups 7 and 8, belonging to the C2 classification (Table 2).

Group 1 is richest in species (100) and has a small proportion of introduced species (29%) (Table 3). The ground underneath these plots consists mainly of relatively dry, sandy soil, frequently intermingled with marine shells. Geranium sanguineum L. is one characteristic dominant in this group. Vegetation plots from border zones, i. e., the unploughed and unfertilized areas, all belong to this group. This represents a dry calcareous meadow type of vegetation (cf Hallberg 1971).

Groups 2, 3, 4 represent heterogeneous types of vegetation,

rich in species, but with a large proportion of introduced species. The total number of species lies within the range 45-81 and all groups are dominated by perennial grass species. The soil varies from dry sandy soil to wet humus-rich soil.

Group 2 is dominated by the grasses Poa pratensis L., Festuca rubra L. and Elytrigia repens (L.) Nevski and has a high proportion (47%) of introduced species, belonging to cultivated fields, fertilized hay meadows and pastures (e.g., Anagallis arvensis L., Stachys palustris L., Barbarea vulgaris R. Br. and Ranunculus repens L.).

Group 3 is characterized by a mixture of species from groups 1,2 and 4. This group has no real dominant and several weed species are present (e.g., Polygonum convolvulus L., Polygonum aviculare L., Vicia tetrasperma Schreb. and Viola arvensis Murr.) and also several seed mixture immigrants, such as Galium mollugo L., Holcus lanatus L., Plantago media L., Chrysanthemum leucanthemum L. and Phleum pratense L.. The introduced species account for 47% of the total number of species here.

In group 4, Arrhenatherum elatius (L.) J. et C. Presl. is a dominant. This species accompanied imported seed mixtures for leys in the late 1900s (Souminen 1979) and is currently a dominant in some abandoned fields on Lindö and Kalvö. Other frequent species, such as Vicia cracca L., Anthriscus silvestris Hoffm. and Cirsium arvense Scop., all belong to the group of introduced species, accounting for 44% of the total number of species in this group.

Groups 5, 6 should be looked upon as moist meadow vegetation types. The soil is mainly organic and the subsoil water level is close to the soil surface. The vegetation is dominated by a few tall species. As revealed in the joint classification, none of the plots in these groups was colonized by shrub or tree species (cf. Table 3). Group 5 is dominated by Carex disticha Huds. The total number of species is 26, the I-species accounting for 42%. Group 6 has a very low total number of species (10), and is dominated by Lysimachia vulgaris L., Urtica dioica L. and Filipendula ulmaria (L.) Maxim.

Group 7 and 8 in the C2 classification (Table 2) refer to forested plots and thus have a crown cover >50%. Apart from the vigorous tree colonizations, these groups have very little mutual species relationships. Group 7 is characterized by species growing on wet soils, such as Filipendula ulmaria, and a set of mesic meadow species. The group has a relatively low number of species (57) (Table 3). Group 8 is characterized by a set of species belonging to deciduous, nutrient-rich forests or groves (e.g., Hepatica nobilis Mill., Carex digitata L., Melica nutans L., Poa nemoralis L. and Melampyrum pratense L.). Constant species within this group are Geranium sanguineum and Primula veris L. The group thus exhibits distinct connections with group 1.

4.2. Vegetation ordinations

The reciprocal averaging ordinations of uncolonized plots (Fig. 2a, 2b) indicate two main directions of variation: one

(axis 1) with groups 1 and 6 as end points, and another (axis 2) perpendicular to the first, with groups 1 and 4 as end points. The third axis does not yield any considerable amount of new information. The ordination diagram (Fig. 2a, 2b) confirms the intermediate position of groups 2 and 3 obtained by the C1 classification (Table 1).

Linear regression analysis of the first axis coordinates against figures for humus content expressed as loss on ignition (Fig. 3), shows a significant correlation ($r^2=0.80$; $p < 0.001$). Other soil variables, such as content of macronutrients, carbon/nitrogen quotient and pH, showed no correlation with the axis 1 ordination coordinates. The plot coordinates for the second axis were tested against content of introduced species (Fig. 4) and time from abandonment, but a significant correlation was found only for the first variable ($r^2=0.60$; $p < 0.001$).

In the ordination of the joint set of plots (Fig. 5a,5b) the main variation is expressed along ordination axis 1 with groups 1 and 4 as end points. Groups 7 and 8, containing mainly forested plots, show a tendency to be separated along the second axis. Group 3, almost covered by the positions of the plots in group 2, is separated along the third axis (Fig. 5b). Forested plots are concentrated to groups 1, 7 and 8 with scattered occurrences in groups 2, 3 and 4, but absent in groups 5 and 6, excluded in this ordination - see "Methods".

Coordinates along the first axis for the plots show a significant correlation with percentage of introduced species (Fig.

6a) ($p < 0.0001$, $r^2 = 0.23$) whereas time from abandonment (Fig. 6b) shows no such relationship.

4.3. Number of species and forest colonization

The total number of species per plot and the mean number per m^2 for each of the 67 plots from the joint classification (C2) were compared with the time from abandonment for the respective plots (Fig. 7a, 7b). These analyses showed significant correlations ($p < 0.05$) between increasing time since abandonment of the fields and decreasing total and mean number of species per plot. However, the percentage explained variation in the analyses was low ($r^2 = 0.15$, total species number and $r^2 = 0.13$, mean species number). Separating the data into plots from uncolonized plots and shrubby and forested plots, respectively, showed the same pattern.

The content of introduced species per plot was not related to the time since abandonment of the fields (linear regression n.s.). No difference could be found in content of introduced species, or time since abandonment between uncolonized plots and shrubby and forested plots, respectively. Both the uncolonized and forested plots are scattered in the whole age-spectrum (Fig. 6b).

4.4. Soil conditions and forest colonization

No correlation between soil type and frequency of forest colonization could be detected (Table 4).

5. DISCUSSION

The heterogeneous field layer vegetation (Tables 1 and 2) must, to a large extent, be ascribed to the great variation in soil conditions, ranging from dry and sandy humus-poor soils to clayey and wet organic soils (cf. Olsson 1979). These differences are also demonstrated by the range in loss on ignition for the soil samples and thus implicitly in water holding capacity (Fig. 3).

Vegetation group 1 (Tables 1 and 2) differs from all other groups in its high number of species and its low amount of introduced species (Table 3). Geranium sanguineum is a dominant in this group which contains a majority of resident species belonging to mown meadows. The four sample plots from the border zones were all classified in this group. A possible explanation for this deviation in floristic composition from the other groups could be greater availability of dispersal sources to these species: these fields are surrounded, to a greater extent than others, by former mown border zones.

In the ordination of the uncolonized plots (Fig. 2a, 2b) it is reasonable to assume that axis 1 displays variation in soil moisture, with group 1 as one of the end points containing species characterizing dry calcareous meadows, and the moist-growing Lysimachia-Urtica-dominated group 6 as the other end point. The classification result (Table 1) shows that group 6 has a small number of species and also contains a few dominant species, but it is not completely separated from the

other groups as might be interpreted from the ordination diagram (Fig. 2a, 2b). The correlation with introduced species for the second axis (Fig. 4) indicates that this axis displays the variation in remaining "cultural influence".

For the plot ordination of the joint data set (Fig. 5a,5b) the variation along axis 1 should be related to remaining "cultural influence" expressed as percentage of introduced species (Fig. 6a). The configurations of the shrubby and forested plots tending to be distributed along axis 2 suggest that this axis can display "forest influence" (related to canopy cover, etc.) upon the composition of the field layer species. Since the plots from "wet" vegetation types, groups 5 and 6, are excluded from this ordination, the soil moisture gradient here is of little importance.

Tree colonization of the fields, as long as it does not result in a canopy with cover >50%, does not seem to change the composition of the field layer species to any considerable extent. The shrubby and even some of the forested plots were classified in the same groups as the uncolonized plots (Table 2, Fig. 5). As could be expected, plots with a canopy cover >50% had a different field layer composition to a much greater extent (groups 7 and 8 in Table 2). However, groups 7 and 8 displayed a great mutual difference in species composition; group 8 was similar to group 1 and group 7 was most similar to the the "wet" plots in groups 5 and 6 (Table 2), indicating that soil conditions and not tree colonization and forest development was the superior variable for field layer differentiation during the investigated time interval. However,

this difference in field layer composition between groups 7 and 8 can also be interpreted as the occurrence of tree colonization more or less independently of soil conditions. This is further indicated by the lack of correlation between tree colonization and soil conditions (Table 4).

The absence of tree colonization in vegetation groups 5 and 6 (Table 2) indicates that these groups could be resistant to colonization by trees, at least within the investigated time interval; the time from abandonment is 26 - 30 years in these plots (Table 3). The vegetation is here dominated by tall perennials, such as Filipendula ulmaria, Urtica dioica and Carex disticha, which all have vigorous vegetative reproduction by rhizomes or tillers. Their mode of regeneration, with rapid lateral spread, in combination with tall stature, gives them strong competitive ability (Grime 1977, 1981) against invading species.

Several other fields on Lindö belonging to different vegetation groups (Table 2) are still - up to 38 years after abandonment - uncolonized by tree species. All fields in the investigated area were left as leys, provided with a developed sward and litter layer. It is possible that this feature could act analogously to the tall perennials with respect to invading seedlings, viz., as a structural barrier. These old fields may then display a succession path consistent with the "inhibition model" (Connell & Slayter 1977). According to this model, the established species in the field layer function as a barrier against establishment of new seedlings.

Field layer vegetation acting as "metastable" stages for 20 - 40 years was described for Urtica dioica-dominated arable fields (Stählin, Stählin & Schäfer 1972), and for Filipendula ulmaria-communities (Kalela 1961; Stählin, Stählin & Schäfer 1975; Hard 1976; Vinther 1980). Jensen (1978) found the same phenomena with milkweed (Chamaenerion angustifolium (L.) Scop.) in arable fields on the island of Vorsö, Denmark. Wolf (1979) describes abandoned hay meadows, dominated by Deschampsia caespitosa and Arrhenatherum elatius, resistant to tree colonization for more than 20 years.

The overall time interval from abandonment is 38 years, but the difference between the "youngest" and the "oldest" field from abandonment is only 15 years. This may explain the lack of correlation between time from abandonment and tree colonization (cf. Fig. 6b). This interval may be too short to permit meaningful comparisons to be made, especially since the succession started from a sward phase. The heterogeneous soil conditions would further contribute to the complexity of vegetational pattern.

A decreasing number of species correlated to increasing time since abandonment was found, but the relation was rather weak with only 13-15% explained variation in the regression analysis (Fig. 6 and 7). The decrease can be expected to be caused by the degeneration of the populations of introduced species (cf. Hanks 1972; Nicholson & Monck 1974; Hard 1976; Pickett 1982). However, this is not supported on Lindö by any correlation between time since abandonment and occurrence of introduced species. An analysis based on quantitative importance

values for introduced species might have given another result. Bazzaz (1968), Jensen (1978) and Silfverberg (1980) found that the floristic similarity between old fields of varying ages was strong. The changes mainly occurred in the relative importance of species rather than in the floristic composition. However, since the 21 fields analysed in the present study display different phases of tree colonization at the same age since abandonment, with differences of 0 - 100% crown cover, the age-related trends in the composition of the field layer species could be blurred.

6. CONCLUSIONS

The field layer vegetation in the 21 investigated old fields was heterogeneous, in part depending on heterogeneous soil conditions.

No correlation between soil conditions or time from abandonment and tree colonization was detected. Indications were obtained, however, that certain types of vegetation, dominated by tall perennials, were resistant to tree colonization within the available time interval, 38 years after abandonment. Since several other plots belonging to different plant communities were also devoid of tree colonization, it is possible that, irrespective of species composition, the sward may act as a structural barrier against establishment of tree seedlings.

The total number of species per plot and the mean number of species per quadrat in a plot decreased with increasing time

since abandonment, but the content of weeds and introduced species was not related to time of abandonment or to the forest colonization.

The variables discussed in the present paper - structure of the field layer vegetation and soil characteristics - could not be shown to be significantly responsible for the differences in tree colonization. An explanation for the apparent stochastic pattern of tree colonization in the old fields on Lindö should be sought in other factors. Such factors could be the frequency of the tree species adjacent to the fields and the life-history characteristics of these species, especially their mode of regeneration. These factors will be dealt with in forthcoming papers (Olsson 1984a, 1984b).

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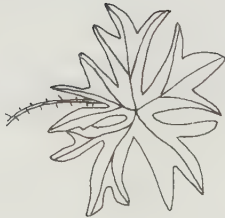
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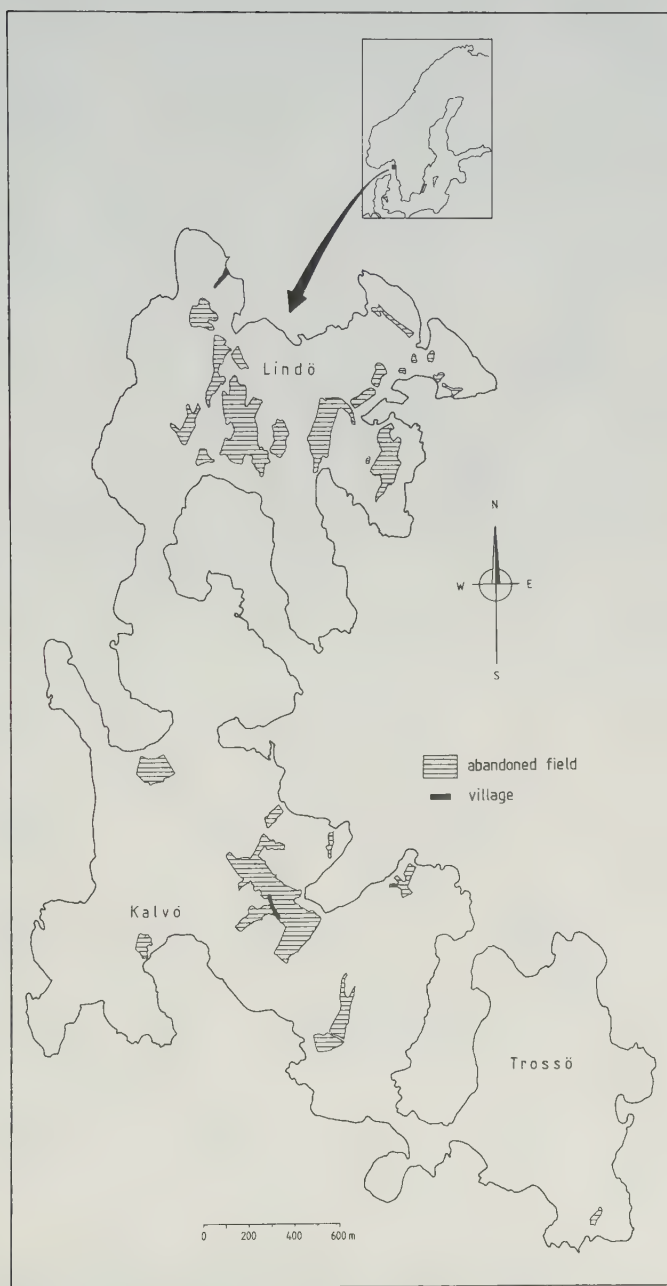


Fig.1. The investigation area, the island of Lindö-Kalvö off the Swedish west coast.

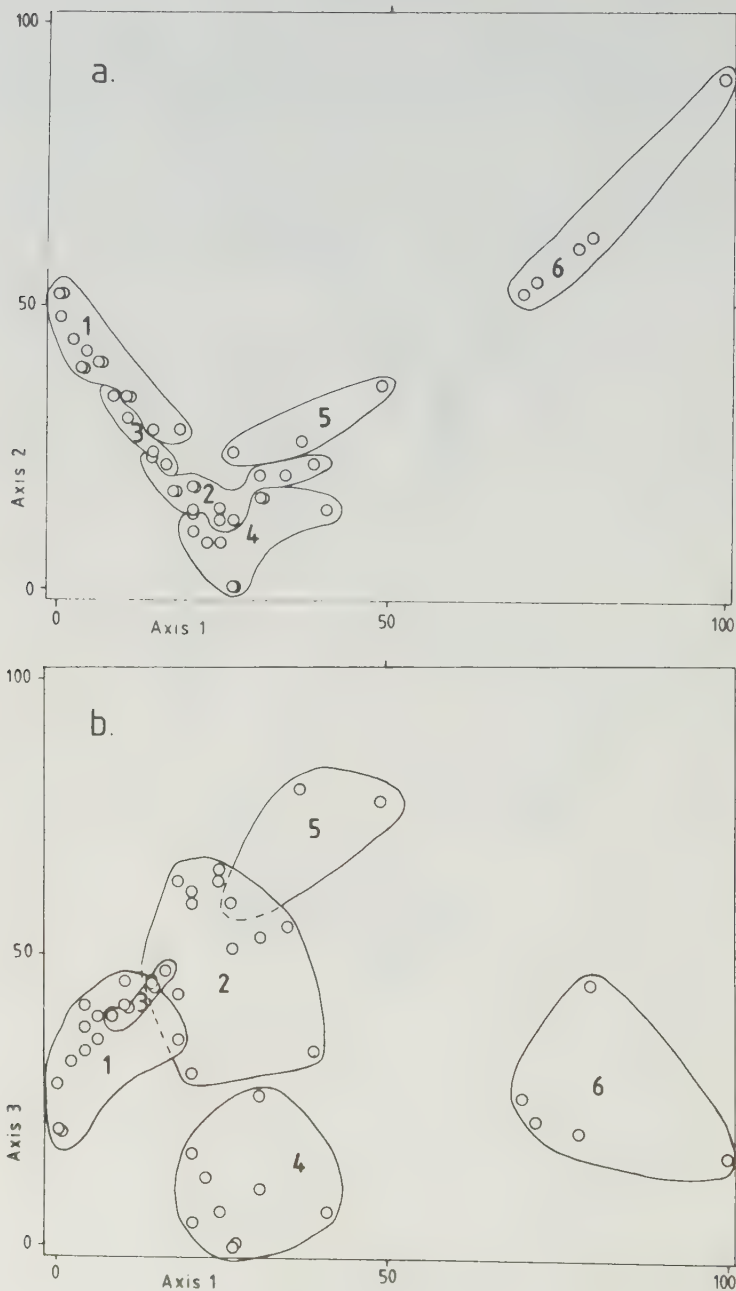


Fig. 2. Reciprocal averaging ordination of plots uncolonized by shrub and tree species. Each plot is labelled with its group number from the classification, C1 (Table 1). a/ axis 1 vs. axis 2 and b/ axis 1 vs. axis 3. The estimated eigenvalues for the first three axes are 0.717, 0.559, 0.439.

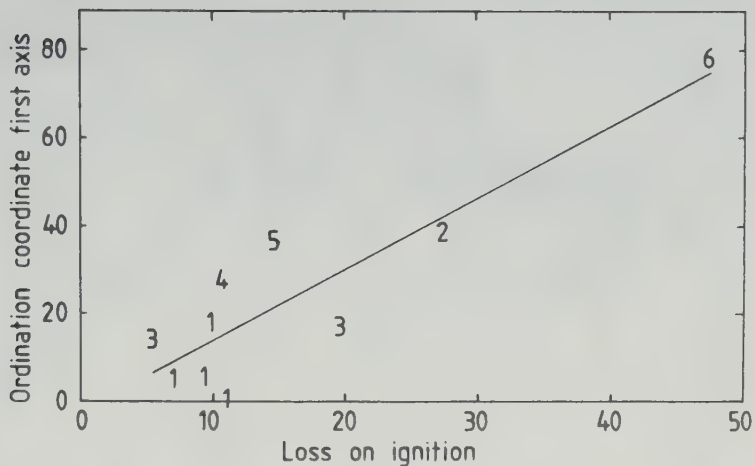


Fig. 3. Correlation between humus content, measured as loss on ignition (percent of dry weight), and coordinates along the 1st ordination axis for plots, uncolonized by shrub and tree species. $r^2=0.80$; $p < 0.001$. Numbers refer to group numbers from the classification, C1 in Table 1.

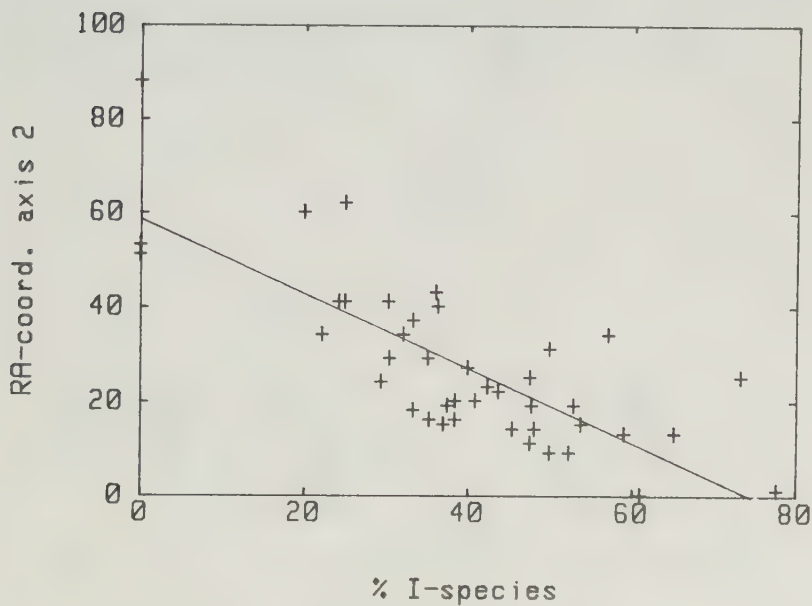


Fig. 4. Correlation between percentage of introduced field layer species (see "Methods" for explanation) and coordinates along the 2nd ordination axis for the plots, uncolonized by shrub and tree species. $r^2=0.60$; $p < 0.001$.

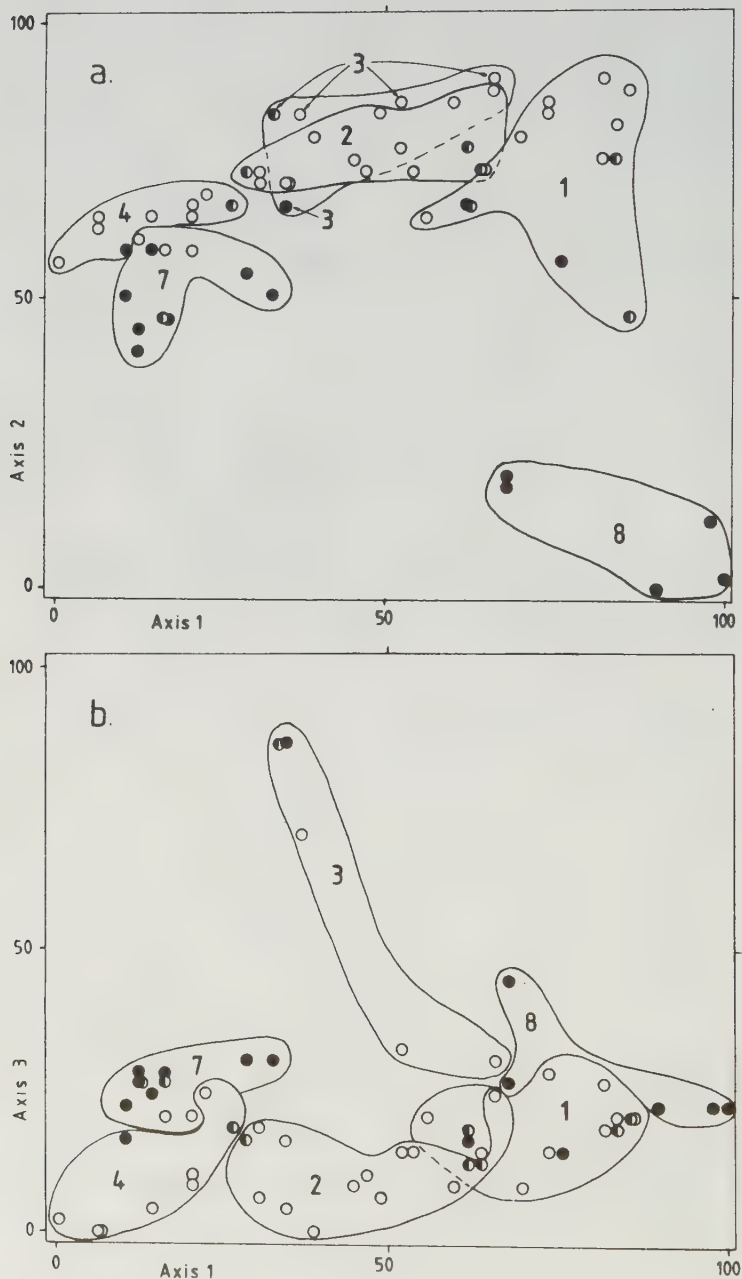


Fig. 5. Reciprocal averaging ordination of plots, uncolonized (open circles) as well as partly colonized (semi-filled circles) or forested (black circles) by shrub and tree species. Each cluster is labelled with its group number from the classification, C2 in Table 2. Groups 7 and 8 are excluded from this ordination - see "Methods" for explanation. a/ axis 1 vs. axis 2, and b/ axis 1 vs. axis 3. The estimated eigenvalues for the first three axes are 0.557, 0.439, 0.383.

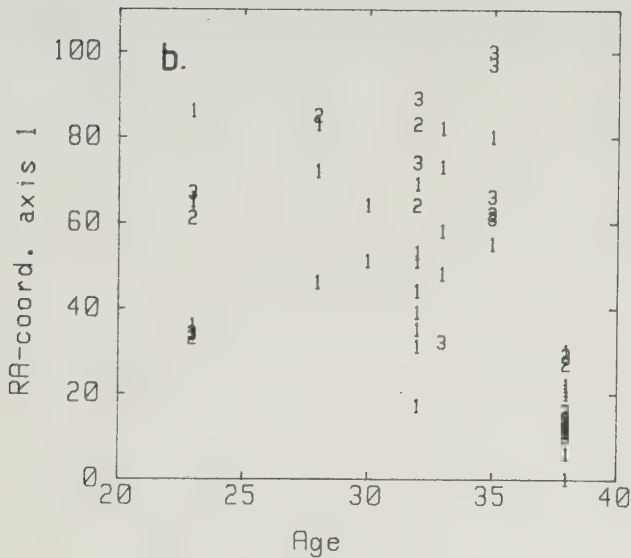
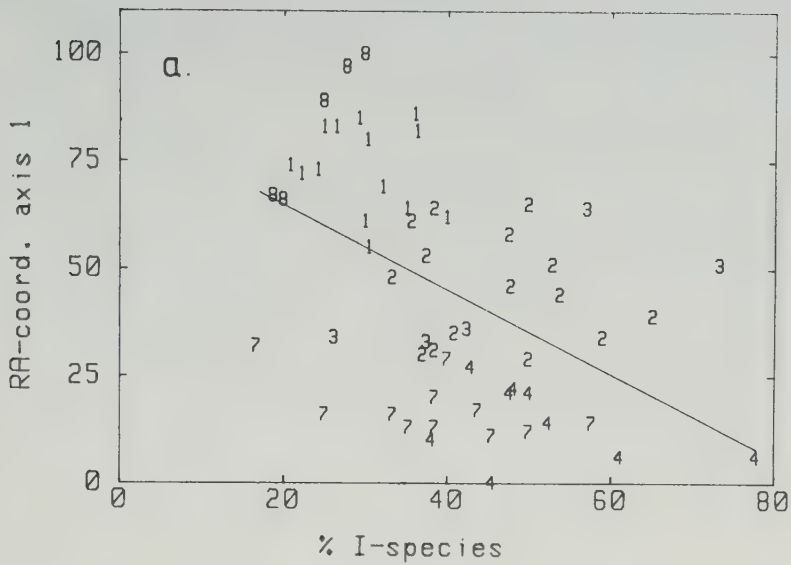


Fig. 6. Correlation between coordinates on ordination axis 1 for plots, and a/ content of introduced species ($r^2=0.23$; $p < 0.001$); b/ time from abandonment (n.s.). Both uncolonized as well as shrubby and forested plots are included in the analyses, but plots from groups 7 and 8 in the classification, C2 (Table 2) are excluded. Labels in a/ refer to group numbers from the classification, C2 in Table 2. Labels in b/ refer to: 1=uncolonized plots; 2=shrubby plots; 3=forested plots.

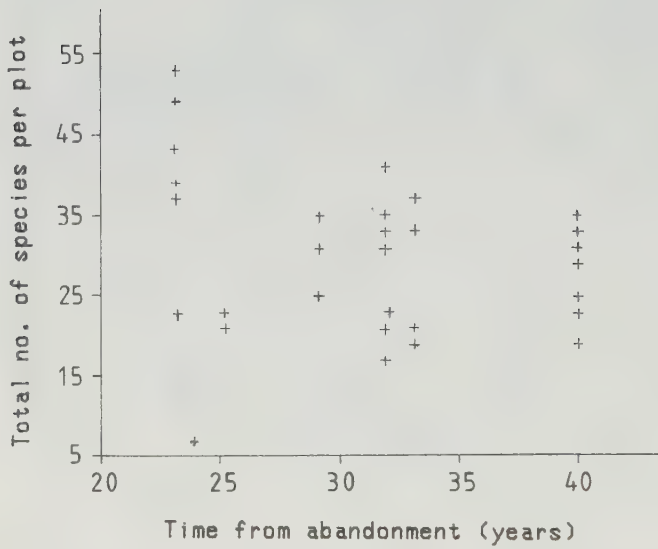


Fig. 7a. Correlation between total number of species per plot and time from abandonment; all plots: $r^2=0.15$; $p < 0.05$.

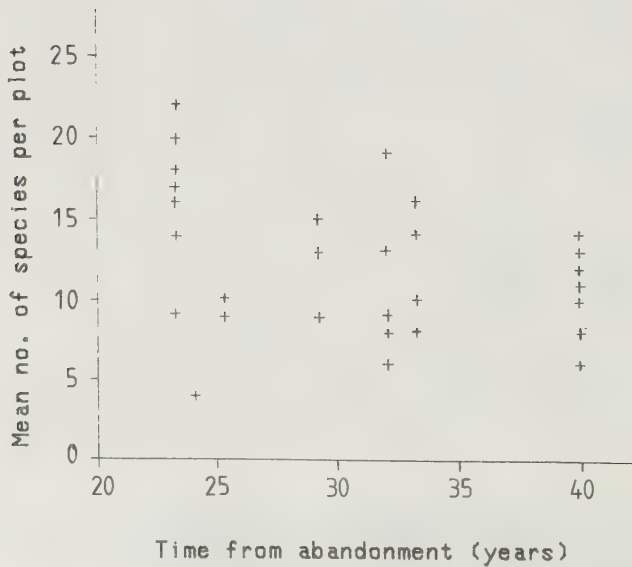


Fig. 7b. Correlation between mean number of species per m^2 and time from abandonment; all plots: $r^2=0.13$; $p < 0.05$.

Table 1. Classification, C1, of plots uncolonized by shrub and tree species. I = 'introduced species' - see 'Methods' for explanation. The classification is based upon arithmetic mean cover per plot of field layer species. Fusions stopped at similarity ratio 0.31. Next fusion would be that of groups 2 and 3. Species nomenclature follows Lid (1974).

Vegetation group		1	2	3	4	5	6
Column no.		1...5...11...	.5....21...5		31...5...	.41	...5.
	<i>Galium verum</i>	1131312332+.	+.+.+.+.+.+	2211	.1..1....	.1.	
	<i>Arrhenatherum pratense</i>	++112112+12+1	+.+.+.+.+.+	1+11		..	
	<i>Pimpinella saxifraga</i>	111111111+1	+.1.....	1+1.		..	
	<i>Silene nutans</i>	+11++1+11+1++	+.+.+.+	+.+		..	
I	<i>Rumex acetosa</i>	...1.+1+.+++	+.+.+.+.+.+	1+1+	+.+.+.+.+	..	
	<i>Trifolium medium</i>	...+.211.1+.	+.3..		++.34.3+	..	
I	<i>Centaurea scabiosa</i>	1...+.++12+.	+.2.1.....	1+1.		..	
	<i>Carex caryophyllaea</i>	.1+++.2+221++	+.+.+.+	..		..	
	<i>Thalictrum minus</i>	...+.11+111..+	..3+.....	1+.		..	
	<i>Hypericum perforatum</i>	+.2+1.++.+.+	+.+.+.+	..	.1.....	..	
	<i>Galium boreale</i>	3+.1+1.....+		..	.1+.1..+	..	
	<i>Festuca ovina</i>	+.2+313221..		.1.		..	
	<i>Primula veris</i>	+.+.+.+++1111		..		..	
	<i>Fragaria viridis</i>	+.+.++1.+1...	+.+.+.+.+.+	+.+		..	
	<i>Anthoxanthum odoratum</i>	...2.2+2..+.+		1..		..	
	<i>Briza media</i>	+.111.1		+.+		..	
	<i>Viola canina/riviniiana</i>	...1.11+++...		..1		..	
	<i>Filipendula vulgaris</i>	...+.1+412....		..		..	
	<i>Poa pratensis</i>	334+3.1+21.12	315252542141	1241	+.1..111+	212	1+..
I	<i>Achillea millefolium</i>	+11112111+++1	+21.+...1+.	322.	+.11+.1+.	+.+	
I	<i>Vicia cracca</i>	1.++1+++.1+1+	+14+...+.1++	..11	1+221+.1+	..	
	<i>Dactylis glomerata</i>	+.+.+.21.1122	14+1143.12..	1122	+.11+.121.	+.+	
I	<i>Galium mollugo</i>	+.+.+.+.+.113	232.244331+1	+.+	11+11+1..	11.	
I	<i>Elytrigia repens</i>	1.2...+.+.11	4436.1135321	111+	11+..++...	22.	
	<i>Festuca rubra</i>	...+.+.1.+...1	1+1.45451.1+	1213	+.+.1...	22+	
	<i>Geranium sanguineum</i>	4545555445554	+11+...+.+.+	3+.		.2.	
I	<i>Medicago lupulina</i>	+11.2..+111++	...++121....	++1.		..	
	<i>Centaurea jacea</i>	+.+.+.1+.1111	+.1.+...2..	..1.	.1+.22.1.	..	
	<i>Lathyrus pratensis</i>	2.1.....113	3+11+122.11	...+	.11+.212	431	1....
I	<i>Cirsium arvense</i>	+.+.+.+.+.1	2.....233321	...+	221321112	.3.	+.+.+
I	<i>Equisetum arvense</i>	+.1+	+.+.1...+.+1	11+1	+1++	..	
	<i>Agrostis tenuis</i>	+11....	+.2+	4325	.1+.312.	..	
	<i>Fragaria vesca</i>	+.+.+.+.+.++	1..		++1+1+.	..	
I	<i>Arrhenatherum elatius</i>		+.+.+.+.+.+		556552235	..	
I	<i>Ranunculus repens</i>		+.+.11++...			..	
I	<i>Anthriscus sylvestris</i>	+++.+.+.+.+.+	+2..1...23.1	.1+1	212222112	..	
	<i>Carex spicata</i>	+.+.+.+.+.+.+	...++11...+.+	+.1		..	
I	<i>Tragopogon pratensis</i>		...+++.+.+	+++.+	+.+.+.+.+	..	
	<i>Festuca pratensis</i>	.1+.+.+.1.	...+.+.+.+.+	.1.1		++.	
I	<i>Knautia arvensis</i>	...11..1+.+.+	+.+.+.+.+.+	1+.		..	
I	<i>Trifolium repens</i>	...+.+.+.+.+	+.+.+.+.+.+	+++.+		..	
I	<i>Sedum maximum</i>	...11++...	+.+.+.+.+.+	111.		..	
I	<i>Taraxacum vulgaria /coll</i>	...+.+.1.	+.+.+.+.+.+	+++.+		..	
I	<i>Arrhenatherum pubescens</i>	...+.1.1.	...+.+.+.+.+	++.		..	
I	<i>Plantago lanceolata</i>	...+.11+	...+.+.+.+.+	+.1.		..	
I	<i>Vicia tetrasperma</i>	...+.+.+.+.+	...+.+.+.+.+	++.		..	
	<i>Lotus corniculatus</i>	...1.+...	...+.+.+.+.+	..1		..	
	<i>Urtica dioeca</i>	...+.+.+.+.+	...+.+.21+.	..	.1...1.4	.1	5314.
	<i>Filipendula ulmaria</i>	...+.2.	...+.2+.36	..1	...+.34+	++	235.+
	<i>Geum rivale</i>	...+.2.	...1.+.		...+.2341	..	1....
	<i>Carex disticha</i>		...+.+.+.+.+			536	1.+4+
	<i>Lysimachia vulgaris</i>		...1.			..	35346
I	<i>Trifolium arvense</i>	...1.		1+.		..	
I	<i>Viola arvensis</i>			1++.		..	
I	<i>Allium vineale</i>			++.		..	

Table 1. cont.

Vegetation group	1	2	3	4	5	6
Column no.	1...5....11..	.5....21...5		31...5...	.41	...5.
I Rumex acetosella			++		...	
I Holcus lanatus			+.1		...	
I Polygonum aviculare			+.+		...	
I Cerastium fontanum			++		...	
I Polygonum convolvulus			+.+	+++		
Ranunculus acris	+.+	+	.1	++		
I Stachys palustris		+.+.1+			...	
Heracleum sphondylium		+.1+			...	+
Rubus idaeus		+		1.....		
I Glechoma hederacea		+.+			...	
Inula salicina	1	1.			...	
Agrostis stolonifera		3.....+.+			...	
Potentilla anserina		+.+	1		1.+	
I Achillea ptarmica		+		+.1.		
Campanula rotundifolia	..++1.....					
Agrimonia eupatoria	++		+.+	1.....		
I Chrysanthemum leucanthem	+.+.	+.+	+		...	
I Trifolium pratense	+.+.+	+.+	+		...	
Campanula trachelium	1.....+.+		+		...	
Origanum vulgare	2.....+.1.+				...	
I Rumex crispus		+.+	1	+.	+	
Anthyllis vulneraria	1+.11.		+		...	
I Alchemilla glaucescens	+.11+				...	
Hieracium pilosella	++11....		+		...	
Linum catharticum	+.11.+				...	
I Plantago media	+.11.+		+.+		...	
Luzula campestris	...1.+.1.+.+		+		...	
Sieglingia decumbens	...+.11.1....		+		...	
I Phleum pratense	1+....	+.+.+	+	+.+		
Campanula persicifolia	+.11.1.....	+.+	+		...	
Stellaria graminea	...1..+.	+.+	1	+.++		

Additional species. For each species column number:cover score.

(I) = introduced species.

Valeriana sambucifolia 35:++; (I) Stellaria media 35:++; Scrophularia nodosa 35:++; (I) Artemisia absinthium 27:++; (I) Verbascum thapsus 30:++; Vicia silvatica 5:1; Galium uliginosum 23:++; Bothrychium lunaria 5:++; (I) Barbarea vulgaris 22:++; Tripleurospermum maritimum 13:++; (I) Anagallis arvensis 20:++; (I) Hieracium vulgatum 6:++; Melampyrum cristatum 1:1; (I) Myosotis arvensis 14:++; Carex flacca 11:++; (I) Prunella vulgaris 11:++; Potentilla erecta 11:++; Molinia coerulea 29:1; (I) Rhinanthus angustifolius 29:++; Angelica sylvestris 29:1; Ophioglossum vulgatum 29:++; Carex otrubae 40:++; Polygala vulgaris 10:++; (I) Hypochaeris radicata 10:++; Potentilla tabernaemontani 10:++; Poa compressa 18:++; (I) Vicia sepium 18:++; Hypericum maculatum 28:1; (I) Euphorbia helioscopia 19:++; Ranunculus polyanthemus 5:+, 9:++; (I) Arabis hirsuta 9:1, 11:++; (I) Galeopsis bifida 13:+, 29:1; Deschampsia caespitosa 29:+, 40:++; (I) Mentha arvensis 14:+, 34:++; Hypochaeris maculata 6:1, 10:++; (I) Cirsium vulgare 16:+, 29:++; Veronica chamaedrys 1:1, 6:++; Epilobium sp. 15:+, 32:++; Hepatica nobilis 1:+, 13:++; Armeria maritima 4:+, 9:++; (I) Agrostis gigantea 27:+, 39:1; (I) Atriplex patula 22:+, 27:++; Carex hirta 5:+, 26:++; (I) Arenaria serpyllifolia 5:+, 26:++; Trifolium campestre 5:+, 26:++; Veronica officinalis 4:+, 6:1; Juncus conglomeratus 35:+, 38:2; Rubus saxatilis 4:1, 6:1 Sedum acre 5:1, 9:++; (I) Sonchus arvensis 14:+, 20:3, 21:2; Deschampsia flexuosa 4:3, 6:2, 8:+.

Table 2. Classification, C2, of plots uncolonized as well as colonized (c) by shrub and tree species. I = 'introduced species' - see 'Methods' for explanation. The classification is based upon arithmetic mean cover per plot of field layer species. Fusions stopped at similarity ratio 0.47. Next fusion would be that of groups 1 and 2. Species nomenclature follows Lid (1974).

Vegetation group	8	1	2	3	4	7	5	6
Column no.	1...5 cccc	...11...5... .C....C...C.CC	21...5....31... .C....C....C	5.... .CC	41...5... .C.C.C.	.51...5... CCC.CCCCC.	61. ...	.5.
I								
<i>Fragaria vesca</i>	+. + + +	+. + + +	1...11		++1++1+	..1..2..+.	...	
<i>Hepatica nobilis</i>	23211	+1.....2....1+	+.			+.....	...	
<i>Taraxacum vulgaria</i> /col1	+1.	+. +. 1.....	++..+.	+++++			...	
<i>Carex digitata</i>	.22.1	2....+					...	
<i>Melica nutans</i>	112+1	+. 1.					...	
<i>Solidago virgaurea</i>	+ + + +	+. 1.					...	
<i>Poa nemoralis</i>	+ + 2	1.					...	
<i>Ribes rubrum</i>	+ + + +	+ +.	+ + +.				...	
<i>Melampyrum pratense</i>	+1.1.						...	
<i>Convallaria majalis</i>	11111						...	
<i>Geranium sanguineum</i>	+12.	44545544554234 +111++1.1++1+	+. 111+. 2. +. +.	3+. 1.			...	
<i>Silene nutans</i>	1123.	+1...2.+1223+2	1.14+121343.122	11211	++11.1+21.	++221.132.1	+	
<i>Dactylis glomerata</i>	1111	+. +. +. +. 2111123	2+432. +2344331+	+. +.	11+1+11+.	1+11+.	11.	
<i>Primula veris</i>	1111+	1+. +. 1111. 1	+. +. +. +.				...	
<i>Pimpinella saxifraga</i>	.11..	1111111++..+1	1.1+. 1. 1.				...	
<i>Galium verum</i>		1113231+. + + +	+. 1.	221.	1. 1+		1.	
I								
<i>Centaurea scabiosa</i>		11. +11+. +. + +	+. 2. 11+	1+			...	
<i>Arrhenatherum pratense</i>		+1+121+2+..1	2. 2. +. 1+	1+1+			...	
<i>Carex caryophylla</i>		11+. +2. 1+					...	
<i>Lathyrus pratensis</i>	++...	21.1...+111+13	31+++1.11+122..				1.	
<i>Vicia cracca</i>	+. +.	11.+1+. 1+. 1+	++114+1.1...+11				...	
I								
<i>Medicago lupulina</i>	.11..	+1112.111+. 1+	1.+1+11221.	++...	1+22111+	11.....	+	
<i>Achillea millefolium</i>		++111111++1+. 1	1+121. 2+. +. 11	32. +.	11++111.	++...+. +.	+	
<i>Centaurea jacea</i>	+2. +. +.	+2112+1	++1. 1+. 2.	1.	1+. 222.		...	
<i>Poa pratensis</i>		31343121.11142	344152454254212	121+1	1.1. +. 11+	1.1. +. 11	212	1. +.
I								
<i>Elytrigia repens</i>		1. 2. +. 1+. 1.	4234361. +113534	11+.	11+. + + +.	11.....	22.	
<i>Festuca rubra</i>		+. + + + 1+	11+1. 1415451. +	123. 2.	+. +. +. 1.		22+	
<i>Carex spicata</i>	+. +.	+. +. +. +. 1.	+. +. +. +. 121. +.	1. 1.			+	
<i>Urtica dioeca</i>							...	
I								
<i>Anthriscus sylvestris</i>	+. +.		+. +. 2. +. 1.	11+1	1.1. +. 4	1.12. 211.	1.	5314.
I								
<i>Equisetum arvense</i>		+. +. +. 11+. +.	++1. +. 1+. +. +.	111. +	21212222	1112223211	+	
I								
<i>Rumex acetosa</i>	+. +.			1+1+			+	
<i>Ranunculus acris</i>				1+1			+	
<i>Festuca pratensis</i>				11. 1			++.	

[illegible]

Poa trivialis 62:++; (I) *Cirsium palustre* 62:++; (I) *Veronica serpyllifolia* 58:++; *Geum urbanum* 56:++;
Pteridium aquilinum 54:4; *Juncus conglomeratus* 47:++; 59:2; (I) *Alchemilla monticola* 47:++;
Valeriana sambucifolia 47:++; *Scrophularia nodosa* 47:++; 57:1; *Rubus idaeus* 40:1, 44:1, 46:1, 50:1, 58:++;
(I) *Verbascum thapsus* 40:++; 49:++; *Epilobium montanum* 34:++; 46:1; *Glechoma hederacea* 33:++; 34:1, 58:++;
Galium uliginosum 33:++; (I) *Barbarea vulgaris* 32:++; *Viola mirabilis* 5:1; *Carex pallescens* 4:++;
Rubus saxatilis 2:2; (I) *Stellaria media* 2:++; 4:++; 47:++; 50:1, 55:1, 57:++; *Carex nigra* 38:++;
Luzula multiflora 38:++; 46:++; (I) *Achillea ptarmica* 33:++; 38:++; 41:++; 47:1, 56:1; *Potentilla*
erecta 14:++; 38:1; *Rubus fruticosus* /coll 1:++; 15:1, 33:1, 44:++; *Equisetum pratense* 1:2, 2:++; 38:1;
Anemone nemorosa 1:++; 4:1; (I) *Lapsana communis* 1:++; 55:++; 57:1; *Geranium robertianum* 1:++; 55:1;
(I) *Rhinanthus angustifolius* 37:++; 39:1; *Angelica sylvestris* 37:1, 38:1, 50:1; (I) *Prunella vulgaris*
2:1, 4:++; 13:1, 14:++; (I) *Vicia sepium* 3:++; 5:++; 27:++; (I) *Cerastium fontanum* 26:++; 34:++; 37:++;
39:++; 50:++; (I) *Polygonum convolvulus* 26:++; 40:++; 42:++; 43:++; 45:++; *Agrimonia eupatoria*
1:1, 13:1, 15:++; 19:++; 26:++; 38:++; 45:1, 51:++; *Lotus corniculatus* 12:++; 13:++; 26:++; 37:1, 39:1;
Sieglingia decumbens 11:1, 26:++; 38:++; 39:++; *Stellaria graminea* 11:++; 33:++; 37:1, 39:++; 44:++; 45:++;
46:++; 50:++; 52:++; 59:++; (I) *Rumex crispus* 32:++; 37:1, 42:++; 50:++; 60:++; *Ranunculus polyanthemus*
10:++; 12:++; *Sedum acre* 10:1, 12:++; (I) *Arrhenatherum pubescens* 11:1, 12:1, 26:++; 27:++; 28:1, 36:++;
(I) *Agrostis gigantea* 36:++; 60:1; (I) *Atriplex patula* 2:++; 36:++; *Anthoxanthum odoratum* 11:++; 14:++;
19:++; 35:1, 39:++; *Luzula campestris* 11:++; 14:++; 18:++; 35:++; *Carex hirta* 10:++; 34:++; 35:++; 50:++;
(I) *Arenaria serpyllifolia* 10:++; 35:++; (I) *Trifolium campestre* 10:++; 35:++; (I) *Plantago lanceolata*
11:++; 12:1, 26:1, 35:++; (I) *Rumex acetosella* 35:++; 36:++; (I) *Allium vineale* 13:++; 35:++; 36:++;
Hieracium pilosella 11:++; 12:1, 13:++; 35:++; (I) *Trifolium arvense* 10:1, 35:1, 36:++; (I) *Polygonum*
aviculare 26:++; 34:++; 35:++; (I) *Viola arvensis* 26:++; 35:1, 37:++; *Epilobium* sp. 4:++; 23:++; 42:++; 57:++;
Rubus caesius 18:1, 22:++; 28:2; *Poa compressa* 13:1, 22:++; 26:++; *Alchemilla glaucescens* 11:++; 13:1,
14:1, 15:++; 22:++; (I) *Anagallis arvensis* 22:++; 30:++; *Hypericum maculatum* 22:++; 26:1; *Festuca*
ovina 7:1, 8:++; 10:++; 11:1, 12:2, 14:1, 26:1, 38:++; *Carex flacca* 7:++; 14:++; *Briza media* 7:3, 11:++;
12:1, 13:++; 14:1, 19:1, 22:1, 26:++; 28:++; *Satureja vulgaris* 7:++; 13:2; (I) *Knaulia arvensis*
5:++; 7:++; 10:1, 12:1, 13:++; 18:1, 19:++; 22:1, 24:++; 26:++; 28:++; 35:1, 42:++; 50:++; (I) *Arabis hirsuta*
7:++; 12:1, 14:++; *Campanula rotundifolia* 7:1, 9:++; *Anthyllis vulneraria* 7:++; 10:1, 12:1, 26:++;
Heracleum sphondylium 1:1, 5:++; 21:1, 32:++; 38:++; 56:2, 57:2, 58:++; 63:++;

Appendix to Table 2. Additional species. For each species column number: cover score.

(I) = introduced species.

Group	No of quadrats	No of plots	Mean no. species /group	Total no. species /group	Total no. I-species /group	% I-sp. /group	Mean time from abandonment
C1:							
1	84	13	14.06 ±1.33	100	29	29	29.9 ±1.25
2	103	12	9.89 ±0.83	74	35	47	31.6 ±1.00
3	43	4	15.37 ±1.70	81	38	47	26.5 ±2.02
4	75	9	8.77 ±1.04	45	20	44	38.0 ±0
5	20	3	7.15 ±1.13	26	11	42	30.0 ±3.00
6	30	5	3.20 ±0.55	10	2	20	26.4 ±1.60
C2:							
1	128	14	11.68 ±1.42	91	28	31	30.8 ±1.17
2	133	15	13.00 ±1.81	92	39	42	30.9 ±1.22
3	57	5	8.96 ±1.36	83	38	46	25.8 ±1.71
4	87	9	12.24 ±1.41	53	23	43	38.0 ±0.00
5	20	3	7.15 ±1.13	26	11	42	30.0 ±3.00
6	30	5	3.20 ±0.55	10	2	20	26.4 ±1.60
7	64	11	13.08 ±1.06	57	21	37	37.2 ±0.58
8	39	5	9.79 ±1.40	53	17	32	32.0 ±2.33

Table 4. χ^2 -test of the distribution of plots colonized by shrub and tree species in relation to soil type. Null hypothesis assumes equal colonization on all soil types.

Soil type	Number of plots	Colonized plots		Deviation (D=O-E)	D ² /E
		Observed frequency (O)	Expected frequency (E)		
Sand	44	21	21.67	- 0.67	0.0207
Clay	17	10	8.37	1.63	0.3174
Wet organic soil	6	2	2.96	- 0.96	0.3115
Total	67	33	33.00	0	$\chi^2=0.6496$ n.s

III. OBSTACLES TO BIRCH COLONIZATION IN OLD FIELDS

ABSTRACT

Two abandoned fields left as leys on a small island off the Swedish west coast 31 and 39 years preceding the investigation, were used for an experimental study of Betula establishment. Although there was access to adjacent birch seed sources, the old fields lacked birch colonization. Plots cleared from field layer vegetation were exposed to spontaneous birch seed rain. Seed rain, seed germinability and soil conditions were also examined. In one of the fields, Betula seedlings colonized the plots and survived for more than one year. In the other field, with soil of lower water-holding capacity, no seedlings appeared and neither did sowing result in any colonization. It is concluded that two different factors acted as obstacles to birch colonization: 1/ the grass sward as a structural and competitive barrier, and 2/ soils with a low humus content, and thus low water holding capacity.

1. INTRODUCTION

The Betula species (Betula pubescens Ehrh., Betula verrucosa Ehrh.) in Scandinavia are generally considered as pioneer species colonizing forest clear-cuttings, forest-fire areas, burn-beaten lands (Sarvas 1948) as well as abandoned fields (Kalela 1961). The small, wind-dispersed Betula seeds have a low amount of stored energy (Sarvas 1952, Björkroth 1972). Besides, Betula is dependent on seed reproduction for colonization. The birch seedlings are thus very sensitive to competition and drought (Sarvas 1948, Miles and Kinnaird 1979a) and need patches in which competition is low, in combination with soil and climatic conditions offering enough moisture during seedling development. Sarvas (1948) considered 50 - 100 cm² as a minimum size of patch for the successful establishment of birch seedlings.

The small island of Lindö-Kalvö off the Swedish west coast contains 26 old fields, abandoned during the period 1942 - 1957 (Olsson 1984a). In 1981, one-third of the fields were dominated by deciduous forest, consisting mainly of Populus tremula L., with some elements of Quercus robur L., Fraxinus excelsior L. and Tilia cordata Mill. One-third had developed a shrub stage dominated by Prunus spinosa, Rosa and Crataegus species, and the remaining fields were dominated by perennial herbs and grasses. Although there was access to adjacent seed sources none of the old fields was colonized by birch. The arable fields were all left as leys with an established sward at the time of abandonment. In

contrast, abandoned pastures on the islands were colonized by forests of Betula or Pinus.

On this island, the various obstacles to colonization by Betula in the old fields may be:

- 1/ lack of seed sources and germinable birch seeds;
- 2/ competition with field layer vegetation;
- 3/ drought.

The present study was performed to investigate if any of the above-listed obstructing factors could explain the lack of Betula colonization in the old fields of Lindö and Kalvö.

The work is a part of a study dealing with the factors influencing secondary forest succession on the coastal island of Lindö (Olsson 1984a: field layer species structure, soil conditions; 1984b: access to diaspore sources, regenerative strategy).

2. MATERIALS AND METHODS

2.1. Investigation site

The study was performed on the island of Lindö-Kalvö ($58^{\circ}47'N$, $6^{\circ}54'E$), in the northern part of the Swedish west coast archipelago. A general description of the investigation area is given in Olsson (1984c). Two abandoned fields uncolonized by birch (fields F1, F2), but with adjacent birch seed sources, were studied (Fig.1) in comparison with two birch-dominated abandoned pastures (P1, P2). The old fields and abandoned pastures are surrounded by formerly grazed,

rocky plateaus dominated by Calluna heathlands with increasingly large groves of Populus tremula, Betula species and Pinus sylvestris L.

The time of abandonment for each field and pasture was determined by interviewing the landowners.

Field F1 is completely lacking in trees and shrubs, and the field layer vegetation is dominated by perennial grasses, mainly Festuca pratensis Huds., Elytrigia repens (L.) P.B. and Agrostis tenuis (L.) Sibth. The shortest distance to seed-producing birches is 25 m (Fig. 1). Field F2 is characterized by scattered Rosa shrubs. The field layer vegetation is dominated by Arrhenatherum elatius (L.) J. et C Presl. Seed producing birches grow along the western border (Fig. 1).

In 1981 pasture P1 (Fig.1) was dominated by birch forest, consisting of a mixture of Betula verrucosa and Betula pubescens. At the time of abandonment there were some birches along the western border of the pasture. Pasture P2 is also covered by birch forest, with Betula pubescens as the main constituent. Seed sources for this forest are presumably birches along field F2 as well as some scattered birches south of P2 (Fig. 1).

The time from abandonment (counted from 1981) was 31 and 39 years for F1 and F2, respectively, and 25 and 39 years for P1 and P2.

2.2. Experimental design

2.2.1. Seedling establishment and survival

The effect of the sward as a colonization barrier was studied in field F1 and F2 by manipulating the sward in randomly distributed plots, 0.5 x 0.5 m in size, surrounded by a buffer zone of 0.3 m, treated like the plots. The experimental plots were exposed to one of the following treatments: (a) removal of the sward, leaving the upper humus layer exposed; (b) simulated grazing by cutting the vegetation to 2 cm above-ground and wounding the sward with a stick; (c) keeping the vegetation intact, as reference. The distribution of plots in the experimental series is listed in Table 1. In field F1, one experimental series (A1) was prepared for natural seed rain 30 m from seed sources. This series was prepared on August 16, 1980 and the treatments were repeated on August 20, 1981. During May - September 1981 and 1982 the plots were analysed monthly for seedlings.

Another experimental series (A2) was prepared on the same field and sown (20,000 birch seeds/m²; 44% germinability) on September 6, 1980, to ensure sufficient amount of birch seeds. The seeds originated from birches close to field F1. The treatments and sowing were repeated on the same plots in August 1981 (seeds collected in 1981). The plots were examined for seedlings monthly from May 1 to August 1 1981, and from May 1 to August 1 1982.

In field F2, experimental series B1 for natural seed rain was laid out parallel to the field margin, 10 m from seed producing birches. The possible sheltering effect of Rosa shrubs

on birch colonization during natural seed rain was tested by series B2 located beneath each of five different groups of shrubs, 15 m from the seed sources (Table 1). The series B1 and B2 were prepared on August 20, 1980 and examined for seedlings monthly from May 1 to August 30, 1981 and from May 1 to August 30, 1982. Series B1 was extended by five plots where the sward had been removed and five reference plots on August 9, 1981.

2.2.2. Seed-producing birches at time of abandonment

From aerial photographs taken by the Swedish Land Survey Administration in 1936, 1954, 1963, 1971, the amount and species of surrounding groves and trees for each field and pasture were determined. Age determinations by increment borings at stem bases were performed on birches presumed to have been seed producing at abandonment at the four sites. In addition, 10 of the largest colonizing birches in the pastures P1 and P2 were cored to determine the time of commencement of colonization.

2.2.3. Quantity and quality of birch seed rain

During 1980-81, the birch seed rain in field F1 was sampled by 14 traps distributed at 5, 30 and 60 m from seed producing birches; the traps consisted of synthetic grass mats, measuring 0.3 x 0.4 m, densely covered with 2-cm-high blades. Trapped seeds were collected every second week during the period August 30 - October 25 1980. The traps were then left in the field until May 1, 1981, when the accumulated winter and spring seed rain was determined.

Traps of another type were used in 1981 in both field F1 and F2; the traps consisted of square boards (0.3 x 0.3 m) mounted on posts 35 cm above ground. The trap surface was covered with plastic sheet, smeared with vaseline. The sheets were changed and the trapped seeds counted weekly during the period August 2 - September 9, 1981 and every third week until October 25, 1981. In field F1, 5 or 10 traps were placed at distances of 5, 30 and 60 m from the seed sources. The last two positions coincide with those of the experimental series A1 and A2. In field F2, traps were distributed at 10 m and 15 m from seed sources, five at each distance coinciding with the experimental series B1 and B2.

Seed-germination ability was determined (methods in Holmes 1971) on seeds collected from 10 birches close to field F1 and F2, respectively, in early September 1980 and in August 1981 (only F1).

2.3. Soil analysis

For determination of ignition loss, pH, nitrogen and carbon content, five soil cores (volume 203.6 cm^3) were taken in early September 1982 from the humus layer (0 - 5 cm) adjacent to the experimental series (see 2.2.1.) in the two old fields. Ignition loss was determined gravimetrically by drying to 400°C . For nitrogen determination, a semimicro Kjeldahl-digestion was used. Soil carbon content was analysed by means of a "Leco carbon determinator CR 12" (Leco Corp., Michigan, U.S.A.). pH was determined in KCl solution. Since soil conditions in the pastures might have changed considerably since

abandonment, due to colonizing birch forests, soil sampling was not performed here.

3. RESULTS

3.1. Soil conditions

The soil profile for field F1 was characterized by a humus layer of 5 cm overlying a sandy soil slightly intermingled with marine shells. In field F2, the humus layer was thicker, 15 cm, and humus was intermingled to a greater extent in the underlying sandy soil. Marine shells were present from 35 cm and down. The soil analysis showed significantly higher ignition loss for field F2 (Table 2). The carbon and nitrogen contents were also significantly higher in field F2. The C/N quotient was about the same in the two fields, however.

3.2. Seed sources

The oldest cored birch adjacent to field F1 was established around 10 years before abandonment in 1950 (Table 3). The aerial photographs from 1936 and 1954 clearly show the presence of scattered trees. For field F2, a row of birches along the western border is also visible on the same photographs. The oldest sampled tree here was dated to be 32 years old at the time of abandonment in 1942.

At the margins of pastures P1 and P2, the oldest cored birch trees were 45 and 47 years old respectively, indicating ages of at least 20 and 8 years at abandonment. Of colonizing trees in pasture P1 and P2, the oldest sampled trees were 35 and 38

years old, respectively (Table 3).

3.3. Quantity and quality of the birch seed rain

In field F1, the seed rain 30 m from the birches was, on average, only 3% of that at 5 m distance (Table 4). The seed rain in field F2 was about 10 times greater than in field F1 (Table 4). Over the experimental plots, the seed rain during August 1981 in series A1 was approximately 1 % of that for series B1 (mean 22.2 seeds/m^2 vs 2896 seeds/m^2) (Table 4). The seed rain in the unsheltered area (series B1) was not significantly different from that beneath the Rosa shrubs (series B2) in field F2.

In the 1980 seed collection from birches adjacent to field F1 and F2 respectively, 44% and 20% of the seeds germinated. Seeds collected from field F1 in 1981 germinated at an average of 21%.

3.4. Seedling establishment and survival

In field F1, no seedlings were observed during the two seasons of the experiment in series A1. Neither did the sowing experiment in series A2 give rise to any emergent seedling after any of the sowings. Nor did combined sowing and insecticide (against ants) treatment in field F1 result in seedlings.

In field F2, however, the spontaneous seed rain resulted in 4 - 6 seedlings per plot with remown sward in the unsheltered and sheltered series in early August 1981 (Table 5). Of these seedlings, an average of 1.2 (1.4) survived until early August of the second year. That year there was a greater contribution

in June from new germinated seedlings in the unsheltered area, mean 14.6 per plot with remown sward (Table 5) (t-test, $p < 0.01$). However, most of the seedlings succumbed within 5 weeks; the average loss was 97%. At this observation date (August 9 1982), the mean vegetation cover in the unsheltered and the sheltered plots was 75% and 80%, respectively. Vegetatively regenerating grasses were predominant. The mortality during winter 1981 - 1982 was greater beneath the shrubs than for the unsheltered plots, 87% versus 40% (Table 5) (t-test, $p < 0.01$). There were no seedlings in the reference plots at any of the observation dates.

4. DISCUSSION

For field F2 and the pastures, the results agree with the presumed requirements for Betula regeneration listed in the introduction. When the sward was removed in an old field, birch seedlings emerged and some of them survived for more than one year. The mortality of the 1980 seedlings during their first year, less than 50% (Table 5), is low compared with the results obtained by others, 94 - 100% (Miles 1973, Kinnaird 1974, Miles and Kinnaird 1979b). During the summer of 1982, however, seedling mortality was higher (Table 5). In that summer the climate was very hot and dry, compared with long term means for the area (Swedish Metereological and Hydrological Institute 1982). No significant differences in mortality between the unsheltered and sheltered plots could be detected.

Birches at the margin of field F2, 32 years old at the time of abandonment, probably acted as seed sources both for field F2 and for pasture P2. Besides, the birches adjacent to P2 were approximately 8 - 10 years old at the time when grazing ceased (Table 3). As birch can become mature for seed production at ages around 5 - 10 years (Longman and Wareing 1959; observed in western England), these trees could also have functioned as seed sources for P2 at the time of abandonment. The birch forest here, established 1 or 2 years after the grazing was discontinued, is practically even-aged.

Pasture P1 shows a similar trend. It was colonized mainly around abandonment (Table 3) by seeds probably originating from birches in the pasture margin, which had then attained the age of 17 years. Some birches were established in the pasture during the last few years before grazing definitively ceased in 1956. The grazing pressure during these last years was fairly weak due to reduced numbers of cattle.

Hard (1976) reports that fields in southern Germany, abandoned for 20 years, lacked trees although they were within dispersal distance of birch and other species. Miles and Kinnaird (1979a, 1979b) stress the importance of large, grazing herbivores for creating "safe sites" (Harper et al 1961) in grass swards. Mattiasson (1970) and Persson (1982) investigated old pastures in southern Sweden where birch stands were dated close to the time of cessation of grazing, although seed sources were more than 200 m distant. Miles (1973) and Kinnaird (1974) describe heathlands in Scotland, where birch seedlings were almost lacking in intact grass or herb vegeta-

tion but occurred frequently in disturbed spots with bare mineral or humus soil. Kinnaird and Miles (1979a) also report birch colonization of Scottish pastures coinciding with the time of reduced or ceased grazing. This result agrees with the conditions found in Lindö for field F2 and the pastures.

In field F1, no seedling was observed in any of the plots. The soil characteristics of field F1 differ significantly from those in field F2 (Table 2). The sandy, humus-poor soil in field F1 has very poor water-holding capacity. The most important birch seed germination takes place in spring, (personal observation; cf Miles and Kinnaird 1979a). Spring precipitation is relatively low in this area (cf. Olsson 1984a) and the birch seedlings are extremely sensitive to drought and exposure during the germination period (Miles and Kinnaird 1979a, Emberlin and Baillie 1980). One single hot week during this phase can result in up to 100% mortality (Miles and Kinnaird 1979a). Suspected ant predation on birch seeds was not confirmed.

Comparing the seed rain in field F1 and F2 (Table 4), the seed sources for field F1 are situated 25 m outside the field while at field F2 they grow close to the field border (Fig. 1). This results in tenfold higher seed rain over field F2 than in field F1.

In the sowing experiments in field F1 (series A2), the relatively low percentage germination of the seed crop (21 - 44%) should have been compensated for by a high seed supply (20,000 seeds per m²). A probable explanation for the outcome of the

experiments in field F1 may thus be that the soil characteristics unfavourable for birch seed germination, in combination with the low spring rainfall could make it almost impossible for birches to become established at this site.

5. CONCLUSIONS

1/ The grass sward acts as a structural barrier against birch colonization. This is supported by the establishment of birches in experimental plots cleared from the sward in one of the investigated old fields and in pastures densely covered by birch forests dating back to the time of abandonment. Implicit in this argumentation is the presence of safe sites in the sward as a result of cattle grazing and trampling.

2/ Despite the supply of viable seeds and "safe sites" with exposed soil, no establishment of birch could occur in old fields where the soil has a low humus content, and thus very poor water-holding capacity, compared with the first field. The results thus indicate that, although biotic requirements seem to be fulfilled, the great influence of edaphic factors cannot be neglected.

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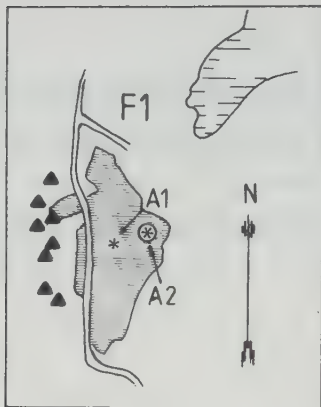
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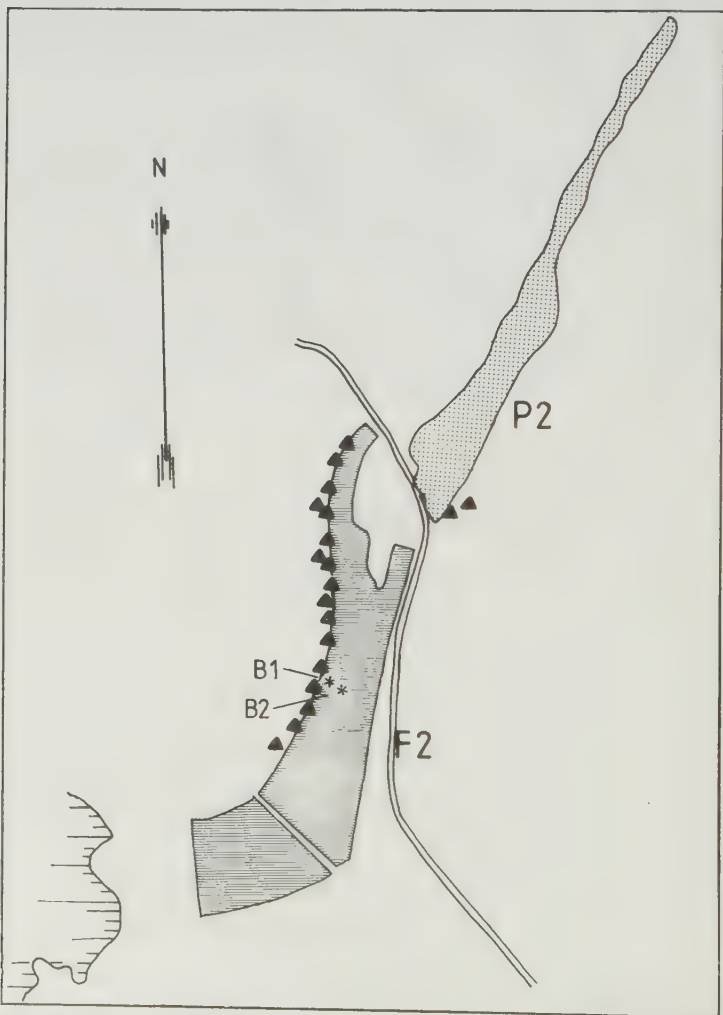
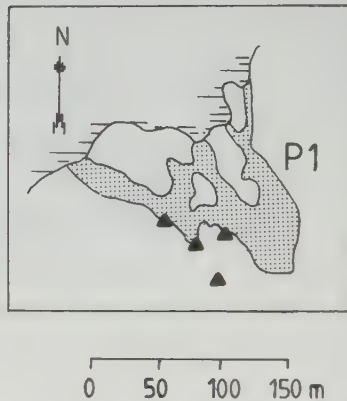


Fig. 1. Positions of the experimental sites in relation to birch seed sources at abandonment (filled triangles). The experimental series A1, B1, B2 were exposed to spontaneous birch seed rain (*) while series A2 was sown with birch seeds (⊗).

Table 1. Survey of experimental design. Treatments and number of replicates in the experimental series A1, A2, B1, B2 in the old fields F1 and F2, respectively. The seed supply was either natural seed rain or sown seed (20,000 seeds per m²). The plots were prepared in August 1980 and series B1 was extended 10 new plots in 1981.

Site	Series no.	Seed supply	Treatments of replicates		
			Removal of sward	Simulated grazing	Reference
F1	A1	seed rain	12	10	10
F1	A2	sown seed	4	4	8
F2	B1	seed rain	5+5	-	5+5
F2	B2	seed rain	5	-	5

Table 2. Characteristics of the upper humus layer (0 - 5 cm) for the abandoned fields F1 and F2 (sample date: September 2, 1982). Ignition loss measured as weight percent. SE = standard error.

Site	pH (KCl)	Loss on ignition (%)	Carbon mg/g dry w.	Nitrogen mg/g dry w.	C/N quotient
Field F1					
Mean	5.65	5.4	26.0	2.12	12.21
SE	0.071	0.45	3.22	0.239	0.422
N = 5					
Field F2					
Mean	5.85	10.9	51.7	4.38	11.83
SE	0.133	0.85	3.88	0.314	0.620
N = 5					
t-test	1.328	5.755	5.092	5.731	0.507
sign. level	n.s.	p < 0.001	p < 0.001	p < 0.001	n.s.

Table 3. Survey of features of the study sites.

	Field F1	Field F2	Pasture P1	Pasture P2
Area (ha)	0.60	0.75	0.50	0.50
Age in yr (1981) since abandonment	31	39	25	39
Land use preceding abandonment	ley	ley	cattle grazing	cattle grazing
Birch seed sources at abandonment	birches 25 m W of the field	birches along the W field border	birches at the W border	birches at E border and about 200m SW of the pasture
Age in yr of oldest seed-source birch (1981)	43	71	42	47
Colonizing woody species 1981	none	aspen clone, Rosa-shrubs	aspen clone, birch-forest	birch forest
Age of sampled colonizing birches 1981 (yr)	--	--	22-35	33-38

Table 4. Number of trapped birch seeds in the abandoned fields F1 and F2. Two types of traps were used; # = plastic mat; \$ = sticky trap; * = both types. SE = standard error.

Site	Distance from seed source (m)	Number of trapped seeds per m2				
		Collection periods:				
		Aug.30- Oct.25 1980	Oct.25- May 1 1980/81	Aug.2- Sept.6 1981	Sept.6- Oct.25 1981	
Field F1	5	Mean	929#	146#	987*	89\$
		SE	679	21	270	22
		N	2	2	7	5
	30	Mean	34#	13#	22*	22\$
		SE	4	4	3	4
		N	10	10	20	10
	60	Mean	13#	17#	18*	--
		SE	13	8	4	--
		N	2	2	7	--
Field F2	10	Mean	--	--	2896\$	122\$
		SE	--	--	667	24
		N	--	--	5	5
	15	Mean	--	--	1796\$	73\$
		SE	--	--	408	35
		N	--	--	5	5

Table 5. Number of emerged seedlings and their survival during the period June 1981 - August 1982 in experimental plots where the grass sward was removed, in field F2. Means for 5 plots are given except for "a" = 10 plots. Standard error is given within brackets. Mortality % counted from the previous observation date. "Unsheltered" (series B1): the plots are situated in an open area. "Sheltered" (series B2): plots situated below Rosa shrubs. "Age": c = current year; c+1 = one year old.

Mean number of seedlings per plot					
Age		1981		1982	
		June 22	Aug 6	June 30	Aug 9
c	<u>Unsheltered</u>				
	Mean	3.2 (+0.92)	4.0 (± 1.05)	14.6a (± 2.19)	0.5a (± 0.16)
	Mortality (%)	--	47	--	97
c+1	Mean	--	--	3.2 (± 1.32)	1.4 (± 1.17)
	Mortality (%)	--	--	40	75
c	<u>Sheltered</u>				
	Mean	5.4 (± 1.47)	6.0 (± 2.05)	4.8 (± 1.93)	1.4 (± 0.51)
	Mortality (%)	--	31	--	62
c+1	Mean	--	--	1.6 (± 0.68)	1.2 (± 0.58)
	Mortality (%)	--	--	87	58

IV. EFFECTS OF REGENERATIVE STRATEGY ON THE INITIAL
PATTERN OF OLD-FIELD FOREST SUCCESSION

ABSTRACT

Factors influencing the process of secondary forest succession were studied on an island in the Swedish west coast archipelago. Twenty-six arable fields and three pastures abandoned 26-41 years ago were investigated. The effect of "number of nearby diaspore sources", "distance to diaspore sources", "regenerative strategy" and "land use" was tested on the number of colonizations for 12 lignous species. Of the total variation, 50% was accounted for by the last three factors. "Regenerative strategy" was the most important (accounting for 36% of the variation), followed by "distance to sources" (22%) and "land use" (4%). Exchanging the variable "distance to sources" for "number of nearby diaspore sources" accounts for 60% of the total variation; "number of sources" contributes 34%.

The dispersal modes ranked as follows in terms of colonization success within the old fields: vegetative regeneration > wind-dispersed group with small seeds > animal-dispersed > wind-dispersed with medium-sized seeds. Under prevailing conditions, with an established sward at the time of abandonment, the wind-dispersed species with medium-sized seeds are successful colonizers only if there are breaks in the sward. The small-sized wind-dispersed seeds attained virtually no successful colonization in the old fields. At distances exceeding 10 m from the dispersal source there is a pronounced decrease in colonizing success for all dispersal groups. The most distance-dependent is the vegetatively

regenerating group, while the animal-dispersed group is the least susceptible. In the pastures, the sward was wounded by grazing and trampling by cattle, which provided numerous safe sites for the wind-dispersed small seeds. Those areas were colonized immediately after abandonment.

1. INTRODUCTION

A number of factors have been shown to influence the process of secondary forest succession in old fields. Such factors are e.g.: last crop in the fields (Beckwith 1954) and soil conditions (Raynal & Bazzaz 1973; Bornkamm & Hennig 1982). It has also been shown that an established sward acts as a structural barrier against forest colonization (Hard 1976; Reif & Lösch 1979; Wolf 1979; Schmidt 1981; Gross & Werner 1982; Goldberg & Werner 1983), supporting the "inhibition" model of succession suggested by Connell & Slayter (1977).

On an island where the number of diaspore sources is limited, the mode of dispersal may, in particular, be an important factor determining which species will become successful colonizers in the old fields. The modes of dispersal are parts of the regenerative strategy which, according to Grime (1981), has "evolved primarily as mechanisms whereby juvenile stages in life histories tolerate or evade the potentially dominating effects of established plants". In this paper the term "regenerative strategy" is used about all forms of regeneration, including sexual regeneration as well as vegetative propagation by suckers.

On the island of Lindö in the Swedish west coast archipelago, 26 arable fields and 3 pastures were abandoned 26 - 41 years ago. Among these areas, tree colonization in 1983 displayed a range of 0 - 100% canopy cover. This paper is one in a series dealing with the factors regulating the

causes of the pattern of forest colonization and vegetational successions in these abandoned farmlands. Previous results from investigated old fields show that the field layer vegetation (i.e., species composition), soil conditions or time elapsed since abandonment could not be shown to have any significant impact on the pattern of forest colonization (Olsson 1984a). The type of former land use was, however, shown to be essential for the colonization success of Betula species (Olsson 1984b). Betula seedlings could easily establish in former pastures, but attained hardly any success in the old fields.

Accordingly, it is hypothesized that the distance between the dispersal sources and fields/pastures, the number of dispersal sources close to the abandoned areas and the reproductive strategy of the species involved are the main determinants of the pattern of forest colonization.

This study was performed to test this hypothesis.

2. MATERIALS AND METHODS

The island of Lindö-Kalvö is situated at 58°47'N, 6°54'E in the Swedish west coast archipelago and comprises a total area of 530 ha. The distance to the mainland proper is 3 km. However, the shore line here is very irregular, with incised inlets and protruding peninsulas. The shortest distance from Lindö to the nearest island is 600 m. Only a number of small skerries exist west of Lindö. The area is close to the

border zone between the nemoral and the boreo-nemoral forest zones (Sjörs 1971; Walter 1979). Mean annual rainfall is 608 mm. February is the coldest month (-1.4°C), and July the warmest (17.5°C) (long-term means for the period 1931 - 1960 on the island of Ursholmen, 10 km north-west of Lindö, Swedish Metereological and Hydrological Institute; official records). Prevailing winds are from the west and north-west. Further characteristics of the investigation area are stated in Olsson (1984c).

On this island, 26 old fields and 3 abandoned pastures - all situated on marine deposits with sand as the main soil constituent - were investigated. The fields and pastures were all abandoned during the period 1942 - 1957. The last crop on all the arable fields was ley during the 2 - 5 years preceding abandonment. The pastures (total area 2.15 ha) were stocked with a total of 15 cattle and 4 horses in rotation grazing before abandonment. The old fields and abandoned pastures are surrounded by extensive areas of rocky outcrops which, at the time of abandonment, were almost devoid of trees and shrubs due to intensive cattle and sheep grazing.

The former land use was classified in two groups: former arable field (ley) and former pasture.

The following 14 ligneous species, acting as diaspore sources on this island, are considered in this paper: Betula verrucosa Ehrh., B. pubescens Ehrh., Salix caprea L., Salix cinerea L. and Salix aurita L. (the

two latter treated together as Salix spp. L.), Pinus sylvestris L., Tilia cordata Mill., Fraxinus excelsior L., Quercus robur L., Sorbus aucuparia L., Malus sylvestris Mill., Corylus avellana L., Populus tremula L.. Subsequently in this paper, these species are referred to only by their generic names. Alnus glutinosa Gaertn. and Picea abies Karst. were also present; but since they were represented by only a few individuals, they were not included in the data interpretation.

From aerial photographs taken during 1936 - 1980 and from field studies carried out during 1980-83, the positions of individuals, assumed to be potential sources of dispersal, were determined for each tree species. Hence, the distance from each dispersal source to the nearest field or pasture border was measured. The following two classes were used: 0 - 10 m; 11 - 200 m. These classes were chosen to represent the immediate border zones of the fields/pastures (0 - 10m) in comparison with more distant positions. A more elaborate classification of distances was also applied but did not reveal any significant relationship.

In addition, the number of groups of dispersal sources close to (0 - 10m) the borders of the fields and pastures was counted. For practical reasons, the number of groups was used instead of individuals; it was judged to be more relevant from the viewpoint of dispersal. The following classes were used: 0, 1, 2, 3 groups.

The tree species were classified into four categories

according to their main regenerative strategy 1/ wind-dispersed species with small seeds (average seed-weight < 10 mg, Björkroth 1972; Bergman 1976) (WS-group); 2/ wind-dispersed species with medium-sized seeds (average seed-weight 10 - 100 mg, Huldén 1941; Wardle 1961) (WM-group); 3/ animal-dispersed species (mainly bird-dispersed) (A-group); 4/ vegetative regeneration (V-group) (Table 1). Evidently, animal predation on seeds is common for all species in group 1 - 3. Small mammal predation on Fraxinus seeds has been shown to be as high as 75% of the yearly seed crop (Gardner 1977); but dispersion and seed burial without consumption is, in general, restricted to group 3.

In all fields and pastures, the number of stems, saplings (> 2 years) or seedlings (< 1 year) for each colonizing species was counted, the following number classes being used: 0; 1 - 5; 6 - 25; 26 - 50; 51 - 75; 76 - 100; > 100 individuals per field/pasture. As the number in the last class often greatly exceeded 100, 200 was used as class midpoint.

The distribution patterns for Tilia cordata and Quercus robur representing the wind-dispersed group with medium-sized seeds and the animal-dispersed group respectively, were studied separately by recording all seedlings and saplings. Six transects, 4 m wide, consisting of continuous rows of 2 x 2 m squares were laid out perpendicular to dispersal sources at the field borders, crossing the fields to the opposite field border.

Each field or pasture was treated as one unit. The mean area for the fields and pastures, ranging from 0.15 to 1.18 ha, was 0.53 ha. The relationship between the number of colonizations and the area of the fields or pastures and the density of the colonizations and area, respectively, was analysed by linear regression.

Four- and three-way analysis of variance was used for the statistical comparison between the groups of variance (Nie et al. 1975).

For time elapsed since abandonment, the age classes were fused to 2 in the final statistical analysis: 25 - 35 and 36 - 45 years after abandonment. A four-way analysis of variance, testing the influence of the variables "time since abandonment", "distance to dispersal source", "land use" and "regenerative strategy" on colonization success, showed no significant main effect of the "time" variable on the number of colonizations. However, the interaction term between the variables "land use" and "time" was significant. The influence of the "time" variable was rejected, however, since the contribution by the "time" variable to the total amount of variation accounted for was less than 0.5 %.

3. RESULTS

Field or pasture area had no influence on number of colonizations ($p < 0.152$, Fig.1). Nor did field or pasture area display any relationship with the density of colonizations, except for the animal-dispersed group where there was a negative relationship ($r^2 = 0.125$, $p < 0.002$).

The "land use", "dispersal strategy" and "distance to dispersal sources" were all significantly correlated to the number of colonizations (Table 2). Totally, 50% of the variation was accounted for in this ANOVA. The "dispersal strategy" was the most important variable, contributing 36% of the total variation. In another three-way analysis of variance, where the variable "distance to dispersal source" was exchanged for the new variable "number of dispersal sources", 60% of the variation in number of colonizations was accounted for. Here the variables "dispersal strategy", "number of nearby diaspore sources" and "land use" accounted for 36%, 34% and 4% respectively of the total variation. The relation between the number of groups of dispersal sources for the different dispersal groups and the number of colonizations are shown in Fig. 2. For the WM-, A- and V-groups in the old fields, the number of colonizations increased significantly with increasing number of nearby sources. On the other hand, irrespective of the number of sources, the wind-dispersed group with small seeds had very little success in the old fields.

The influence of distance from the dispersal source on

colonization was greatest for the vegetatively regenerating species. These displayed virtually no colonization if the diaspore source was more than 10 m distant from the field or pasture (Table 3). If a source from this group is available within a short distance, substantial colonization occurs regardless of land-use type. Highly significant distance-dependent success of colonization was also displayed by the other dispersal modes.

For colonizing success in terms of the number colonizations per field or pasture, the different strategy groups appeared in a different ranking within the land-use types (Table 3). Taking the old fields into account, the vegetatively regenerating group was by far the most successful, followed by the WM-group and the animaldispersed groups. In this case, the small-sized, wind-dispersed seeds had hardly any success (mean 4.9 individuals per field). In the pastures however, the WS-group was far more successful (mean 104 individuals/pasture). Here the V-and the A-groups were equally successful, closely followed by the WS-group. In contrast, the WM-group had very little success here. For this group and for the vegetatively regenerating Populus, any difference in colonization caused by the type of land use could not be detected (Table 3).

The number of colonizations in relation to distance from dispersal source (Fig. 3) reflects the different dispersal modes. Tilia cordata, belonging to the wind-dispersed group with medium sized seeds, displays a peak of progeny near the parent trees (approx. 10 m outside the canopy edge)

(Fig. 3). Quercus robur also has a peak of progeny quite near the canopy, but the acorns are also actively dispersed by animals, reflected by the scattered occurrence of saplings across the fields (Fig. 3).

The frequency of fields with a very low number of individuals (1 - 5 individuals per field) is high for the wind-dispersed group with small seeds (Fig. 4). There are, in addition, only few cases of more than 100 established individuals per field or pasture (Fig. 4), most of them on former pastures (Table 3). In contrast, Populus shows a very strong gregarious tendency, and only rarely one of scattered colonization (Fig. 4).

There was a significant correlation between the number of individuals per field or pasture of the animal-dispersed species Quercus, Sorbus and Corylus (Fig. 5).

4. DISCUSSION

Small seeded wind-dispersed species have almost no possibilities to colonize unbroken sward in old fields (Sarvas 1948; Miles 1973; Miles & Kinnaird 1979a; Olsson 1984b). These species show a high frequency of colonization with a low number of individuals (< 10 individuals per field) (Fig. 4). This is best explained by their ability to become established in small patches of exposed soil in the vicinity of the field edges or open ditches. Here, sometimes there are some spots of broken sward due to overshadowing by trees out-

side the arable field, or by previously established trees in the ditches. The few cases of colonization with numerous individuals (Fig. 4) represent the colonization on former pastures. Here, Betula and Pinus were established in close connection with abandonment (Olsson 1984b). Immediately after the pastures were abandoned there were numerous safe sites (Harper et al. 1965) for the small-sized wind-dispersed seeds. Those sites (breaks in the sward) originated from grazing and trampling by cattle (Merton 1970; Miles and Kinnaird 1979a, 1979b). Thus, such forests are more or less even-aged today (Olsson 1984b; Persson 1982).

At the time of abandonment, the sources of the medium-sized, wind-dispersed seeds, i.e., Tilia and Fraxinus, had relatively higher frequency along the borders of the arable fields compared with the pastures (Olsson 1984c). This feature reflects the great value of these trees in the household economy of the former farmers, who preserved them along the border zones of arable fields, where they were safe from grazing (Merton 1970; Rackham 1980; Olsson 1983a). After abandonment, the trees were no longer coppiced or pollarded; consequently, their canopies grew larger and gradually overshadowed the grass sward, which degenerated and thus provided safe sites for seedlings (Harper 1977; Debussche, Escarré & Lepart 1980; Werner & Harbeck 1982; Green 1983). The progeny of these species were thus able to colonize restricted areas at the borders of the old fields close to the parent trees. This colonization started 10 - 15 years after abandonment (Olsson unpubl.) These species lack the ability to become established in unbroken sward (Merton

1970; Gardner 1976; Wardle 1961). Thus, their colonization in the old fields on Lindö only occurs along the border zones with a degenerated sward close to the parent trees (Fig. 3). This pattern may explain the relatively high colonizing success displayed by this group in such parts of the old fields (Table 3).

Fraxinus seedlings have the ability to persist for a long time as suppressed seedlings and saplings beneath the tree overstorey (Okali 1966; Wardle 1959, 1961; Gardner 1976). In abandoned fields at Lindö provided with a seed-source within a short distance, suppressed seedlings and saplings of Fraxinus are regularly present in the aspen clones. Populus was established here by suckers shortly after abandonment (Olsson unpubl.), permitting the of Fraxinus seedlings to develop in the degenerating sward under the canopy of the Populus clones (cf Werner & Harbeck 1982).

Pigott & Huntley (1978, 1980, 1981) report that, for Tilia, regeneration from seeds rarely occurs in the northwestern parts of the British Isles due to unfavourable summer temperatures for seed ripening. Pigott (1981) concludes that climatic causes also account for the rare presence of Tilia seedlings in central Finland. At Lindö, however, Tilia seedlings occur frequently in the old fields, if there are accessible sites (e.g., gaps in the sward) and a dispersal source within a short distance from the fields. Climatic conditions do not seem to have hindered the dispersion of Tilia on Lindö.

Among the animal-dispersed species, Quercus and Corylus are dispersed by jays and nutcrackers, respectively (Chettleburgh 1952; Morris & Perring 1974; Bossema 1979), but small mammals may also be important (Jones 1959; Tanton 1965; Mellanby 1968; Shaw 1968). Wood-pigeon has also been reported as a disperser of acorns (Jones 1959; Tanton 1965; Mellanby 1968). Malus rely on thrushes frequenting this island, especially during the autumn, but mammals consume the apples and contribute to the dispersal of this species.

Colonization by the animal-dispersed species started immediately after abandonment (Olsson unpubl.). Their relatively great colonizing success further away from the parent trees (Fig. 3) (cf. Mellanby 1968) is a consequence of the habit of birds of hoarding a surplus of seeds in caches and then leaving parts of the caches unconsumed (Bossema 1979). There is evidence that shallow burial of acorns promotes germination, compared with above-ground disposal (Jones 1959; Bossema 1979). Shallow burial also protect the acorns from predation by small mammals (Shaw 1968; Bossema 1979). Quercus acorns as well as Corylus nuts, have substantial endosperm and thus a large amount of stored energy. This enables their seedlings to penetrate a thick litter layer (up to 10 cm, Olsson 1984a) and to compete with the sward species (Jones 1959; Goldberg & Werner 1983).

The association between species within the animal-dispersed group may be due to pioneer trees acting as "nuclei" for subsequent colonization, birds favouring the pioneers as perches (Bechwith 1954; Debussche, Escarré & Lepart 1982).

Pioneer trees increase the structural complexity which, in turn, increases the rate of bird-disseminated seed input into a field by providing recruitment foci (McDonnell & Stiles 1983).

The pattern of the Populus colonization follows logically from its root-sprouting ability, and consequently there is hardly any successful colonization when distance from the source exceeds 10 m (Table 3). The root system of aspen consists of vertical tap-roots as well as extensive horizontal roots capable of protruding 1.5 m per year (Day 1944; Buell & Buell 1959; Barnes 1966). Root-sprouting at distances of more than 35 m from the parent tree has been reported (Barnes 1966; Gifford 1966). But, on the island studied, obstacles to roots are usually present within a smaller distance. The young Populus ramets are supported with nutrients and water from the parent tree (DeByle 1964; Zahner & DeByle 1965) and are thus well fitted for competition with the sward species.

In the absence of nearby diaspore sources for the animal-dispersed and the vegetatively regenerating species, there are old fields in Lindö which - still 30 years after abandonment - have not been colonized by trees. The sward here acts as a structural barrier against the establishment of wind-dispersed species. Uncolonized fields often have a thick litter layer (5-10 cm) and the height of the field-layer vegetation is 50-100 cm (Olsson 1984a). Prevailing conditions at Lindö, where there was an established sward at the time of abandonment, provide a very small number of

accessible sites suitable for colonization by seeds. In the absence of disturbances or other events affecting the sward (e.g., canopy shading by surrounding trees) the development at Lindö corresponds to the "inhibition model" of succession suggested by Connell & Slayter (1977). This model states that "whichever colonizes the site first, holds it against all comers. After all the empty space is filled, invasion is possible only if the new colonist brings its own resources, such as a large seed..." (Connell & Slayter 1977).

It is also possible to apply the succession model of "initial floristics" proposed by Egler (1954), similar to the "tolerance model" of Connell & Slayter (1977). This model states that most species dominating later successional stages arrive at early successional stages and that their later dominance is merely a matter of differential life histories. This trait is valid for Quercus robur as an early colonizer in the old fields at Lindö. Quercus, inhabiting the mature forests in this area, is generally considered to be a late successional species in this climatic region (Sjörs 1971; Walter 1979).

5. CONCLUSIONS

This study has shown the initial pattern of secondary forest succession to be influenced by:

- 1/ the dispersal mode among the colonizing species
- 2/ the number of dispersal sources within a short distance from the fields/pastures
- 3/ the distance from the dispersal source

The different dispersal modes ranked as follows within the old fields: V-group > WM-group > A-group > WS-group (Table 3). Under prevailing conditions, with an established sward at the time of abandonment, the wind-dispersed species with medium-sized seeds are successful colonizers only if there are breaks in the sward. The small-sized wind-dispersed seeds had virtually no colonizing success in the old fields.

At distances of more than 10 m from the dispersal source there is a pronounced decrease in colonizing success for all dispersal groups. The most distance-dependent is the vegetatively regenerating group, which exhibits practically no colonization if the distance exceeds 10 m. The animal-dispersed group is less susceptible to increasing distance from diaspore source than the wind-dispersed group with medium-sized seeds (Fig. 2).

Indications of differences in outcome of colonization, depending on land use, were also found. In the pastures, the sward was wounded by grazing and trampling by cattle, which provided numerous sites for the wind-dispersed small seeds.

Those areas were colonized immediately after abandonment by Betula and Pinus resulting in more or less even-aged stands.

In areas with restricted access to dispersal sources, the dispersal strategy of the available species thus seems to be a crucial factor in determining the pattern of secondary forest succession.

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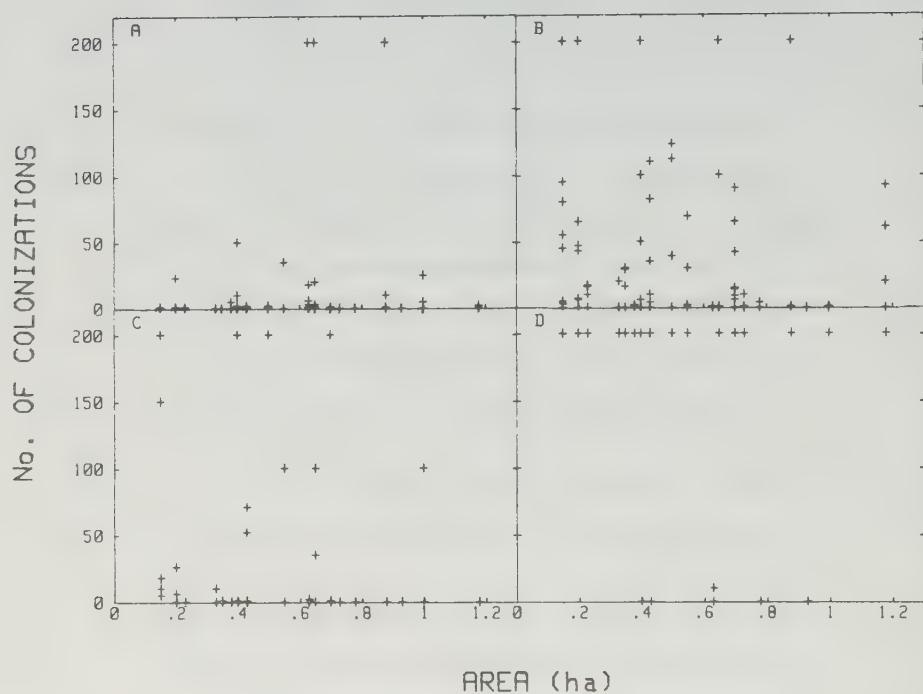


Fig. 1. The total number of colonizations per field or pasture in relation to field/pasture area. A/ wind-dispersed species with small seeds; B/ animal-dispersed seeds; C/ wind-dispersed species with medium-sized seeds; D/ vegetatively regenerating species.

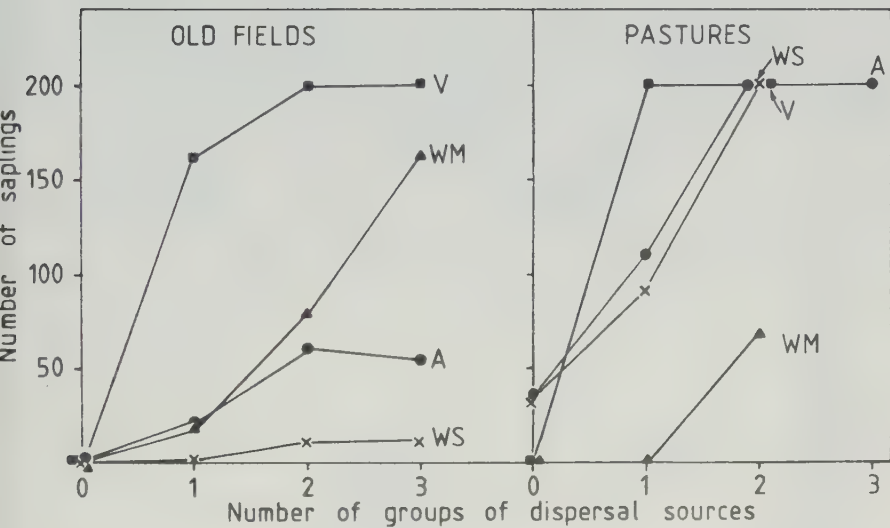


Fig. 2. The number of colonizations per field or per pasture in relation to the number of groups of dispersal sources within the distance 0 - 10 m from the fields/pastures.

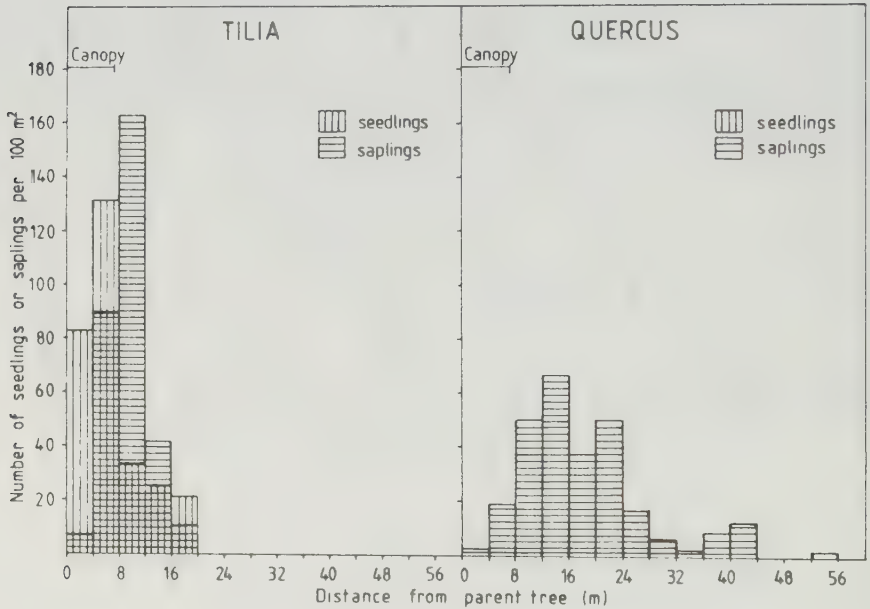


Fig. 3. The distribution of seedlings/saplings along transects in relation to distance from parent trees. The bars represent the means for every 4th m along the transects. The standard deviation is of the same magnitude as the means for each bar. Tilia: $n = 6$; Quercus: $n = 12$.

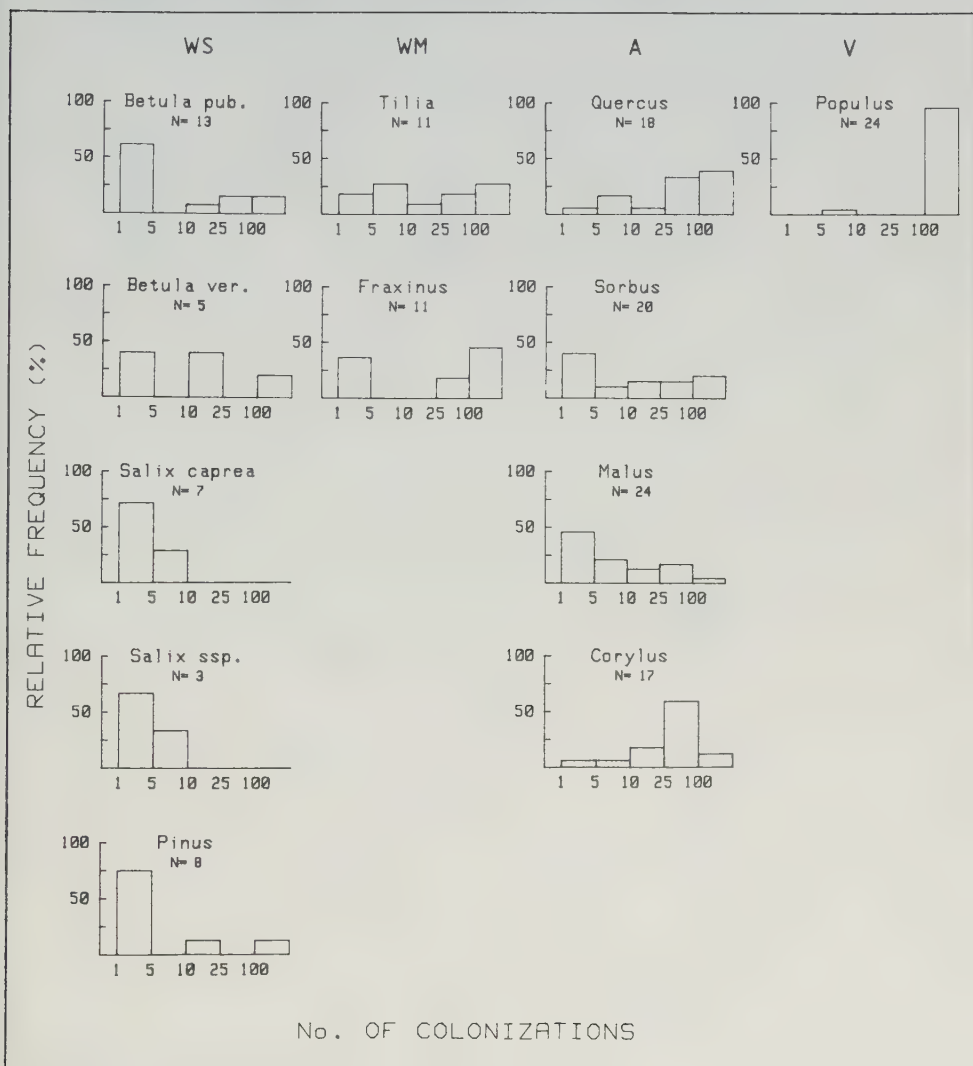


Fig. 4. The relative colonizing frequency distributed on number classes for the ligneous species within the different dispersal groups. WS = wind-dispersed species with small seeds, WM = wind-dispersed species with medium-sized seeds, A = animal-dispersed species, V = vegetative regeneration. The relative frequency is calculated on the total of 26 fields and 3 pastures.

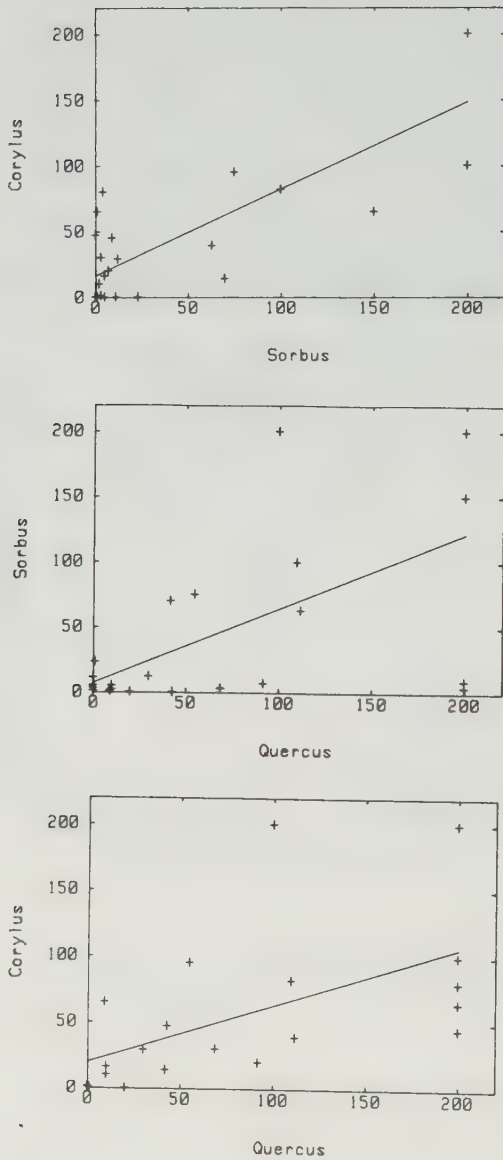


Fig. 5. Correlations between number of colonizations of some animal-dispersed species within the different colonization areas. Only significant correlations are presented.

Table 1. Available dispersal sources in Lindö sorted into groups according to their main regenerative strategy. WS = winddispersed with small seeds; WM = wind-dispersed with medium-sized seeds; A = animal-dispersed; V = vegetative regeneration.

D i s p e r s a l m o d e			
WS	WM	A	V
Betula ver.	Tilia	Quercus	Populus
Betula pub	Fraxinus	Sorbus	
Salix cap.		Malus	
Salix spp.		Corylus	
Pinus			

Table 2. Three-way ANOVA for effect of land use: old field, pasture (LU), distance from dispersal source (DS) and regenerative strategy (RS) on the outcome of colonization in abandoned farmlands at Lindö. Significance levels of F: $p < 0.001$ ***, $p < 0.05$ *. F = F-ratio, i.a. = interaction term.

Variables	Sum of squares	Degrees of freedom	Mean square	F
LU	65321.20	1	65321.20	36.21 ***
DS	167185.04	1	167185.04	92.68 ***
RS	381077.13	3	127025.71	70.42 ***
LU x DS i.a.	21119.01	1	21119.01	11.71 ***
LU x RS i.a.	47982.31	3	15994.10	8.87 ***
DS x RS i.a.	125785.56	3	41928.52	23.24 ***
LU x DS x RS i.a.	14940.56	3	4980.19	2.76 *
Explained	1009857.28	15	67323.82	37.32 ***
Residual	600673.39	333	1803.82	
Total	1610530.67	348	4627.96	

Variables	Percent explained variation	Multiple R ²
LU	4.0	
DS	22.0	
RS	36.0	
		0.499

Table 3. Number of colonizations per field or pasture for the different modes of dispersal in relation to land use and distance to dispersal sources. WS = wind-dispersed species with small seeds; WM = wind-dispersed species with medium-sized seeds; A = animal-dispersed species (mainly bird-dispersed); V = vegetative regeneration. The figures refer to means for the groups and standard deviation is stated within brackets.

Land use	Distance to source	D i s p e r s a l m o d e			
		WS	WM	A	V
Old field	0 - 10 m	4.7 (11.13) n=38	91 (88.75) n=21	44 (55.66) n=75	191 (40.51) n=22
	11 - 200 m	0.2 (0.69) n=93	1.4 (5.15) n=31	1.8 (3.67) n=30	0.0 (0.00) n=3
Pasture	0 - 10 m	105 (102.75) n=8	45 (50.75) n=3	165 (79.16) n=5	200 (0.00) n=2
	11 - 200 m	34.3 (73.84) n=7	1.0 (1.41) n=2	38 (74.26) n=8	0.0 (0.00) n=1

